Restauration de marais temporaires et de pelouses méso-xériques à partir d'anciennes rizières : Rôle respectif des filtres dans l'assemblage des communautés

Isabelle Muller

Université d'Avignon et des Pays de Vaucluse
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THESE

Présentée pour l'obtention du grade de
Docteur de l'Université d'Avignon et des Pays de Vaucluse

Restauration de marais temporaires et de pelouses méso-xériques à partir d'anciennes rizières : Rôle respectif des filtres dans l'assemblage des communautés

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Temporary wetland and meso-xeric grassland restoration on former ricefields: Respective role of filters in community assembly

Isabelle MULLER

Soutenance prévue le 6 décembre 2013 devant le jury composé de :

Anne BONIS	Chargée de recherches, H.D.R. Université de Rennes	Rapporteur
Sharon COLLINGE	Professeur University of Colorado-Boulder	Rapporteur
Armin BISCHOFF	Professeur Université d'Avignon et des Pays de Vaucluse	Examinateur
Gudrun BORNETTE	Directeur de Recherche CNRS Université de Lyon	Examinateur
Elise BUISSON	Maître de conférences, H.D.R. Université d'Avignon et des Pays de Vaucluse	Directrice de thèse
François MESLEARD	Directeur de recherche, Tour du Valat Professeur associé Université d'Avignon et des Pays de Vaucluse	Directeur de thèse

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L'Institut Méditerranéen de Biodiversité et d'Ecologie et de la Tour du Valat

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En particulier,
Hugo et son frère, Norah, Thibaut, et Alba.

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Le rire, nous dit le dictionnaire, est un comportement réflexe, exprimant généralement un sentiment de gaieté, de joie ou d'amusement, qui se manifeste par un enchaînement de petites expirations saccadées accompagnées d'une vocalisation inarticulée plus ou moins bruyante. Aux rires alors, qui sont si profitables dans une vie, et à ceux avec qui on les partage. De l'IUT à la Tour du Valat, de la pause café du matin à la sortie compost, du covoiturage au repas de midi, des trajets à vélo aux pauses café de l'aprem', j'ai été entourée de collègues avec qui il faisait bon rire, et pas seulement. Merci à Renaud avec qui, en dépit de nos divergences, les discussions scientifiques et autres, les randos post-colloques et les fous rires, m'ont pleinement enrichi.

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Table des matières

Table des Tableaux

Table des Figures

Introduction Générale

I.1. Contexte général : le déclin de la biodiversité

La conversion des habitats naturels en zones agricoles, urbanisées ou industrielles, constitue l'un des impacts majeurs de l'Homme sur les écosystèmes. On estime qu'environ 43% de la surface de la Terre ont déjà été directement transformés (Barnosky et al. 2012) et jusqu'à plus de 80% dans les pays industrialisés européens (Primack et al. 2012). En addition des conséquences sociales et esthétiques (Ehrlich and Ehrlich 1992; Meffe and Carroll 1997), les changements subis ont modifié les biens et les services fournis par ces écosystèmes transformés, et constituent une menace pour la biodiversité (Millennium Ecosystem Assessment 2005).

Différents niveaux d'organisation caractérisent la biodiversité : génétique, spécifique, écosystémique (Hunter and Gibbs 2006), dont l'importance pour le fonctionnement des écosystèmes (Hooper et al. 2005) et donc pour le maintien des usages et à terme la survie des civilisations est aujourd'hui largement partagée (Millennium Ecosystem Assessment 2005). Ce déclin généralisé de la biodiversité, par effets directs des activités anthropiques (destruction et fragmentation des habitats, extermination d'espèces et introduction d'espèces invasives), et par effets indirects à travers le changement climatique (Vitousek et al. 1997), est aujourd'hui considéré par son ampleur comme la sixième crise écologique majeure qu'a connue la biodiversité (Barnosky et al. 2012).

Face à la dégradation croissante des écosystèmes (Rands et al. 2010), la restauration écologique apparaît comme une réponse prometteuse (Wilson 1992; Clewell and Aronson 2006; Clewell and Aronson 2007). Cette discipline largement mobilisée pour la conservation (Gauthier-Clerc et al. 2013) est ainsi présentée comme l'une des trois principales actions (gestion, protection, restauration) susceptibles d'enrayer la perte de la biodiversité (Conférence de Nagoya, COP 10, octobre 2010). Parmi les objectifs du nouveau plan stratégique pour la biodiversité défini lors de la conférence des Parties durant la Convention sur la diversité biologique, figure celui de restaurer 15 % des écosystèmes dégradés d'ici 2020 (Convention on Biological Diversity 2011). Pour répondre à cet objectif, l'acquisition de connaissances solides en écologie de la restauration apparaît indispensable.

C'est dans ce contexte que s'inscrit cette thèse, qui via les mécanismes d'assemblage des communautés, teste des moyens de restauration de deux écosystèmes typiques de Camargue après abandon cultural.

I.2. Objectifs et organisation de la thèse

L'objectif général de cette thèse est, pour deux écosystèmes méditerranéens (marais temporaires et pelouses meso-xériques) ayant été soumis à de fortes perturbations anthropiques, (1) de mettre en évidence les principaux mécanismes concourant à l'installation d'une communauté végétale, (2) de tester, pour ces deux écosystèmes, des techniques de restauration et d'en évaluer les conséquences pour les communautés végétales mais aussi pour d'autres compartiments de l'écosystème, notamment les communautés d'invertébrés aquatiques.

Les principales questions abordées dans cette thèse, développée en 4 chapitres, sont (***Figure I.1***):

- Comment définir les écosystèmes de référence? (***Chapitre 1***)
- La restauration des conditions abiotiques permet-elle à la dynamique de la végétation de tendre vers les communautés de référence? (***Chapitre 2***)
- En addition de la restauration abiotique, l'apport de matériel végétal permet-il de restaurer la communauté végétale du milieu aquatique de référence? (***Chapitre 3.1***)
- La communauté d'invertébrés répond-t-elle différemment de la communauté végétale à une opération de restauration? (***Chapitre 3.2***)
- En addition de la restauration abiotique, l'apport de matériel végétal permet-il de restaurer la communauté végétale du milieu terrestre de référence? (***Chapitre 4***)

La première étape dans un projet de restauration est de définir un écosystème de référence que l'on souhaite obtenir ou approcher. Il peut être défini à partir de références historiques, d'enjeux de conservation ou de services écosystémiques recherchés pour le futur écosystème à restaurer. Cette étape permet de poser les objectifs de restauration, de guider les processus de cette restauration et, *in fine*, d'en évaluer le succès (Society for Ecological Restoration 2004; Clewell and Aronson 2007; Miller and Hobbs 2007). Le

chapitre 1 présente la démarche à l'origine du projet de restauration, le site d'étude, ainsi que les bouleversements qu'a connus celui-ci en relation avec ceux qui ont marqué la Camargue au cours des trois derniers siècles. Cette première partie s'attache à définir les écosystèmes de référence et préciser les enjeux de conservation liés à ces écosystèmes, ainsi que le projet participatif dans lequel s'insère ce projet de restauration.

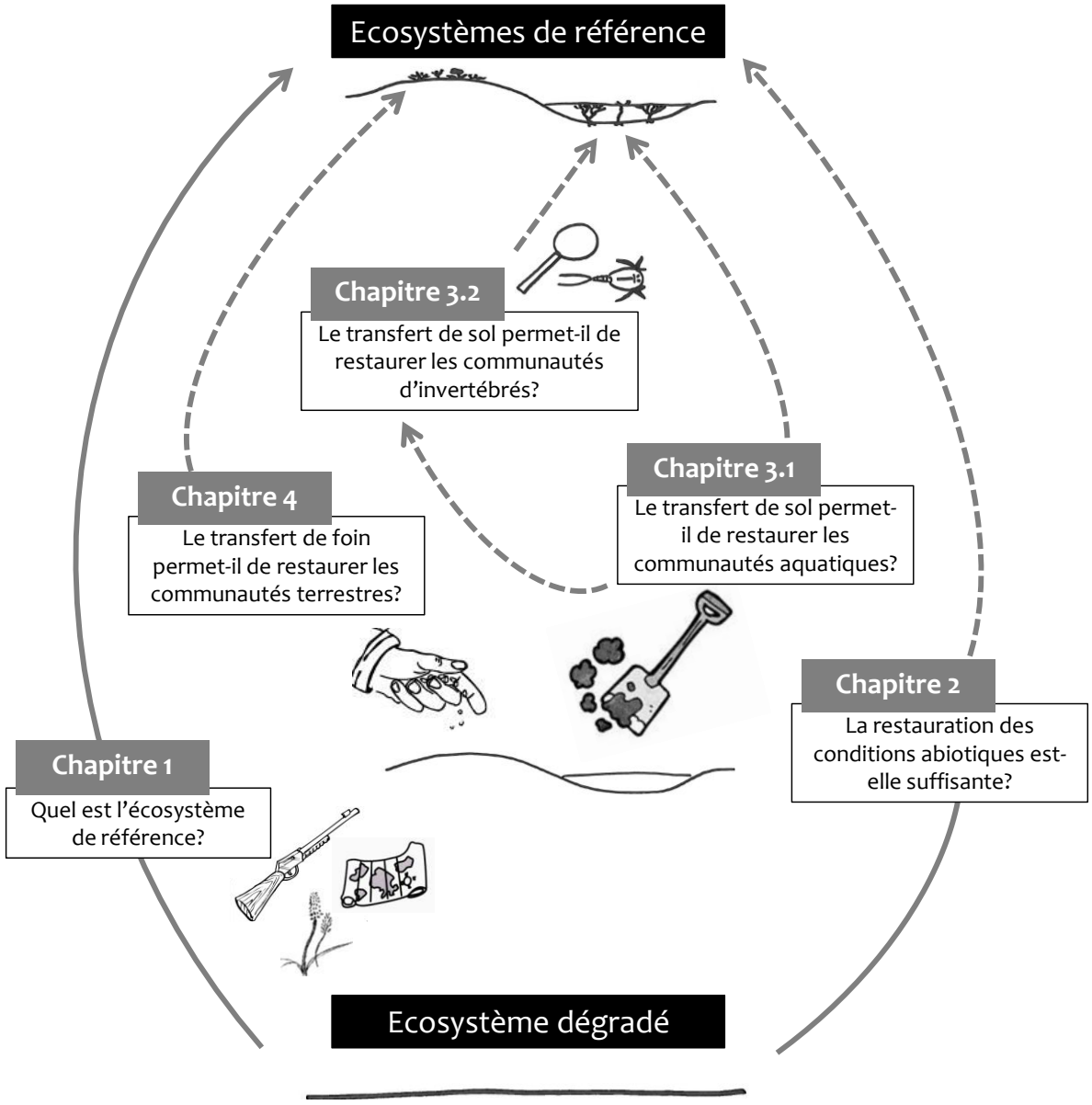


Figure I.1: Schéma général d'organisation de la thèse

La restauration des écosystèmes dégradés, en particulier après l'abandon de l'agriculture intensive, est considérée comme un contexte opportun pour étudier l'assemblage des communautés (Temperton et al. 2004; Cramer et al. 2008; Prach and

Walker 2011). Les modèles théoriques d'assemblage des communautés végétales considèrent que le pool régional des espèces (i.e. espèces disponibles au niveau régional) est soumis à trois filtres : la dispersion des espèces, les contraintes abiotiques, et les relations biotiques (Keddy 1992; Lortie et al. 2004; Guisan and Rahbek 2011). Déterminer le rôle de chaque filtre aide à déterminer les choix dans les traitements à appliquer en terme de restauration (Hobbs and Norton 2004). Après avoir rétabli les conditions abiotiques favorables aux espèces de la communauté de référence (manipulation du filtre abiotique, Prach and Hobbs 2008), l'étude du pool régional d'espèces permet de déterminer la composition potentielle de la communauté. La succession spontanée après la mise en place de conditions abiotiques proches de celles de nos écosystèmes de référence en utilisant l'étrépage de sol est l'objet du ***chapitre 2***. Les résultats permettent d'évaluer la nécessité de forcer la succession végétale vers nos communautés de références.

Quand la succession spontanée ne peut conduire à la communauté végétale de l'écosystème de référence ou s'en approcher (l'écosystème n'est pas sur la bonne trajectoire), une restauration écologique active doit être mise en œuvre (Manchester et al. 1999; Prach and Pysek 2001; Bischoff 2002; Török et al. 2011b). Il s'agit alors de déterminer (1) Comment cette restauration active peut-elle être mise en œuvre ? et (2) Comment les autres compartiments de l'écosystème répondent à cette restauration de la communauté végétale ? Dans les ***chapitre 3.1*** et ***chapitre 4*** sont testées des techniques de restauration efficaces (en terme d'assemblage des communautés) et applicables (i.e. économiquement acceptable à large échelle) en manipulant notamment le filtre de la dispersion. Le ***chapitre 3.1*** concerne la restauration des marais temporaires après abandon d'une culture intensive (riziculture) par l'étrépage de sol et établissement du régime hydrique combiné au transfert de sol collecté dans des sites de référence. Le ***chapitre 4*** concerne lui la restauration des pelouses méso-xériques en combinant étrépage et transfert de foin. Le ***chapitre 3.2*** s'intéresse à la restauration d'un autre compartiment de l'écosystème après le transfert de sol: les communautés d'invertébrés aquatiques; il est l'occasion de discuter les critères d'évaluation du succès de restauration le plus souvent basés sur la flore.

Les études des ***chapitre 2***, ***chapitre 3*** et ***chapitre 4*** ont été conduites en mésocosmes mis en place sur le site d'étude (appelés blocks dans la suite du manuscrit).

La discussion expose les résultats préliminaires de restauration de nos deux communautés à large échelle menée en parallèle de l'étude sur les mésocosmes. De nouvelles perspectives et outils dans la restauration à large échelle sont proposés pour expliquer l'assemblage des communautés notamment en confrontant la théorie déterministe, utilisée dans ce travail, aux théories neutres. Les différents chapitres permettent de comparer les potentialités respectives de la manipulation de filtres d'un milieu aquatique à celle d'un milieu terrestre et la colonisation d'une communauté végétale et d'une communauté d'invertébrés. Enfin sont exposées quelques réflexions d'ordre plus général que soulève l'écologie de la restauration, dans le contexte actuel de perte des milieux naturels et agricoles et de marchandisation de la biodiversité.

La suite de l'introduction générale est consacrée aux concepts et théories scientifiques abordés dans cette thèse ainsi qu'à une présentation du delta du Rhône.

I.3. L'écologie de la restauration

I.3.1. Son origine

La restauration écologique est le processus qui assiste le rétablissement d'un écosystème qui a été dégradé, endommagé ou détruit (Society for Ecological Restoration 2004). Aldo Leopold, à l'origine du premier projet de restauration documenté dans les années 1930 aux Etats-Unis (Jordan and Gilpin 1987) visant à rétablir l'état antérieur des prairies du Wisconsin, appelait ses pairs à devenir des « médecins » de la Terre (Zedler 1999). L'émergence des différentes lois aux Etats-Unis (Loi sur la protection de l'eau: the *Clean Water Act* de 1972; Loi sur les espèces en danger: the *Endangered Species Act* de 1973 ; la loi sur la réhabilitation et contrôle de la surface minière : *Surface Mining Control and reclamation Act* de 1977 ; et la loi de zéro perte nette des zones humides : *Wetland No Net Loss Act* de 1989) a largement contribué au développement de la discipline. En France, l'expression restauration a été employée dès 1860 par le service *Restauration des terrains de montagnes* dont l'activité principale était de reforester les zones dégradées par le pâturage pour lutter contre l'érosion (Combes 1989). Ce n'est qu'à partir de la loi relative à la Protection de la Nature de 1976 et de son décret d'application de 2012, qui impose à tous les projets d'aménagement des études d'impacts et la séquence Eviter-

Réduire-Compenser, et de la mise en place en 1995, du programme national de recherche « Recréer la nature. Réhabilitation, restauration et création d'écosystèmes » que la restauration écologique connaît un véritable essor en France. Aujourd'hui, de nombreux projets de restauration sont mis en œuvre (e.g. différentes syntheses sur des projets de restauration: Walker et al. 2004; Palmer et al. 2005; Benayas et al. 2009; Kiehl et al. 2010; Török et al. 2011b). L'écologie de la restauration, discipline scientifique qui développe et teste un corpus de théories écologiques concernant la restauration d'écosystèmes dégradés (Palmer et al. 1997), fait logiquement évoluer les connaissances théoriques (Bradshaw 1987) et permet d'affiner la pratique de la restauration écologique, en proposant des modèles, des concepts et des outils.

I.3.2. Définition et objectifs

La restauration a souvent été énoncée et perçue comme un ensemble d'actions permettant le rétablissement d'un état antérieur souhaité, qualifié d'initial. Cependant, au fil des expériences, avec le constat d'une quasi impossibilité à rétablir une parfaite réplique du passé (Clewell and Aronson 2007), une vision élargie de la restauration écologique s'est développée; elle fait aujourd'hui plus ou moins consensus (***Figure I.2***). En fonction des objectifs poursuivis, différents termes qualifient les actions de restauration (Society for Ecological Restoration 2004).

La restauration *sensu stricto* est le rétablissement de tous les attributs de l'écosystème de référence, incluant notamment la richesse spécifique, la composition, la structure et la fonction, elle se base donc sur une approche holistique considérant l'ensemble des compartiments, fonctions et services de l'écosystème.

La réhabilitation quant-à-elle se focalise uniquement sur le rétablissement de certains compartiments, fonctions et/ou services, sans par exemple viser le retour de toutes les espèces indigènes (Aronson et al. 1993; Clewell and Aronson 2007). La restauration *sensu stricto* et la réhabilitation se focalisent toutes les deux sur un écosystème historique préexistant. La réclamation, la mitigation, la création ou la réaffectation, à l'inverse de la restauration et de la réhabilitation, visent l'obtention d'un écosystème choisi sans qu'il y ait référence à un écosystème passé. La réclamation et la mitigation sont souvent utilisées dans le contexte industriel afin de répondre à des objectifs et des fonctions utilitaristes (e.g. stabilisation d'un terrain par re-végétalisation) ou à compenser des

milieux détruits (e.g. création de zones humides dans le contexte de banque de ''mitigation'' aux Etats-Unis). La création et la réaffectation transforment un écosystème afin de générer de nouveaux usages de type économique, sociétal ou conservatoire (Society for Ecological Restoration 2004). Dans la suite du manuscrit, le terme restauration sera utilisé dans son acceptation la plus large.

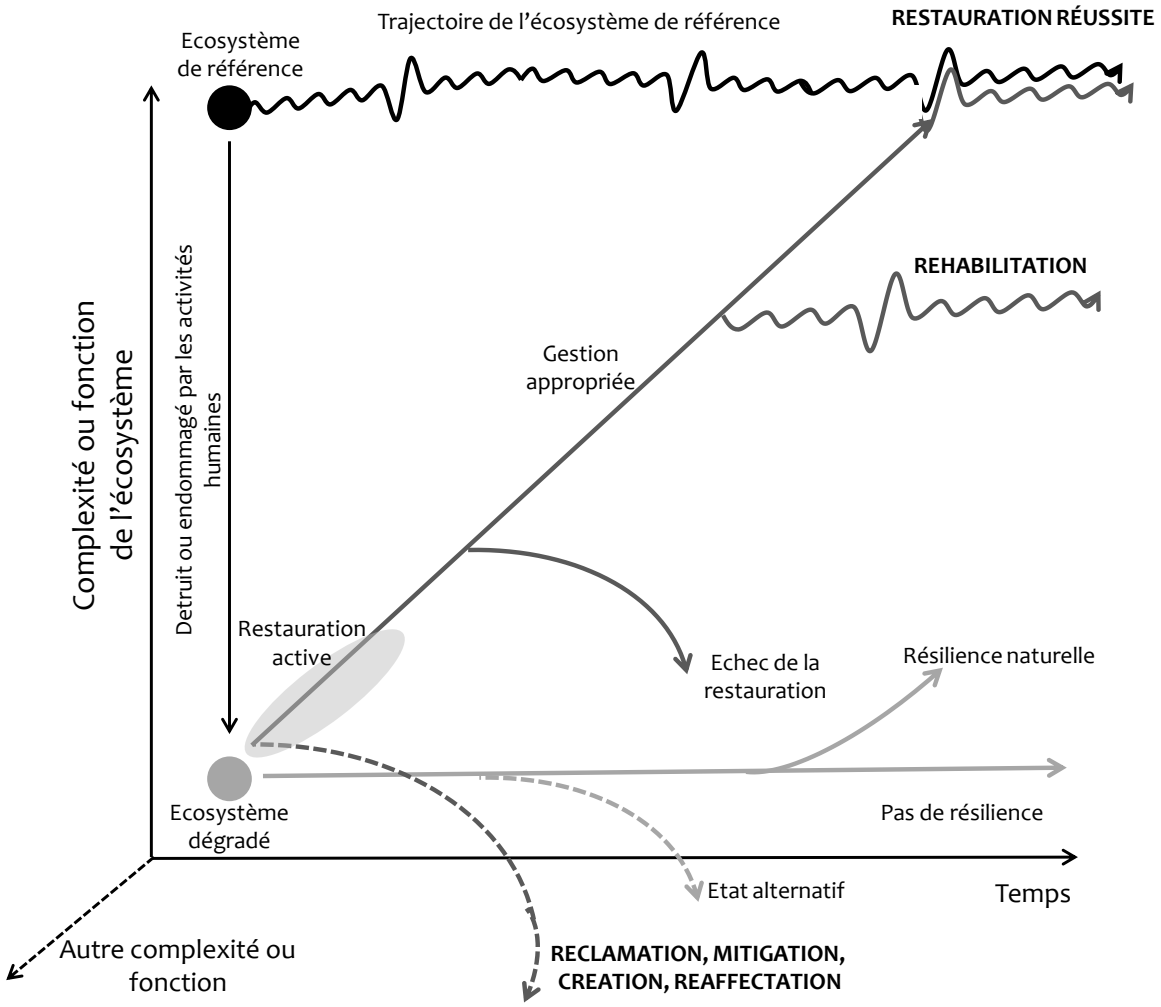


Figure I.2 : Modèle général illustrant les différents termes de restauration, dans un graphique à trois dimensions : temps, complexité ou fonction de l'écosystème de référence, complexité ou fonction d'un autre écosystème. La troisième dimension est représentée par les pointillés. Modifiée de Aronson et al. (1993) et Buisson (2011).

Quel que soit l'objectif visé, la restauration doit prendre en compte la dynamique temporelle des écosystèmes, leur éventuelle résilience à des perturbations et leur tolérance au stress (***Figure I.2***). Les objectifs correspondent donc souvent à une trajectoire de référence (Aronson et al. 1993) elle-même dynamique par les mécanismes

de succession (Aronson and Floc'h 1996; Clewell and Aronson 2007). L'écosystème à restaurer doit être positionné sur la trajectoire successionnelle de référence, avec pour objectif d'obtenir ou de s'approcher de l'écosystème de référence. L'écologie des communautés, au travers des mécanismes de succession, est de ce fait une discipline largement utilisée en écologie de la restauration (Palmer et al. 1997).

I.3.3. L'écologie de la restauration en lien avec d'autres disciplines

Les projets de restauration se basant principalement sur les communautés végétales (Prach and Hobbs 2008), l'écologie des communautés est, comme nous venons de l'évoquer, essentielle à l'écologie de la restauration. La restauration écologique utilisant la manipulation des communautés végétales, une bonne connaissance des facteurs déterminant la dynamique et la structuration des communautés et de leurs rôles respectifs, est nécessaire pour définir les moyens à mettre en œuvre afin de piloter la succession vers l'état de référence et ainsi mener à bien des opérations de restauration (***Figure I.3***, Palmer et al. 1997; Keesing and Wratten 1998; Young et al. 2001; Temperton et al. 2004; Zedler 2005; Falk et al. 2006; Hobbs and Cramer 2007; Cristofoli and Mahy 2010).

La restauration écologique est considéré comme un contexte écologique opportun pour tester des hypothèses (i.e. test à l'acide); les projets de restauration peuvent ainsi substantiellement contribuer à l'avancement des théories fondamentales en écologie (***Figure I.3***, Bradshaw 1987; Keesing and Wratten 1998).

En complément de l'écologie des communautés, de nombreux domaines de l'écologie peuvent être explorés *via* la restauration (e.g. les réseaux trophiques, le fonctionnement des écosystèmes, la paléoécologie, les changements climatiques, l'écologie historique, l'écologie du paysage, etc. Young et al. 2005; Falk et al. 2006), et de nombreux champs autre que l'écologie des communautés végétales peuvent être mobilisés en écologie de la restauration (e.g. dynamique des populations, écologie des communautés d'invertébrés etc.). Une nouvelle discipline récemment apparu en écologie de la restauration est la philosophie de l'environnement, qui apporte d'autres outils de réflexion (e.g. éthique, esthétique, sociétale) à la démarche de la restauration écologique et aux choix de l'écosystème de référence (Light 2009; Maskit 2009; Maris 2010).

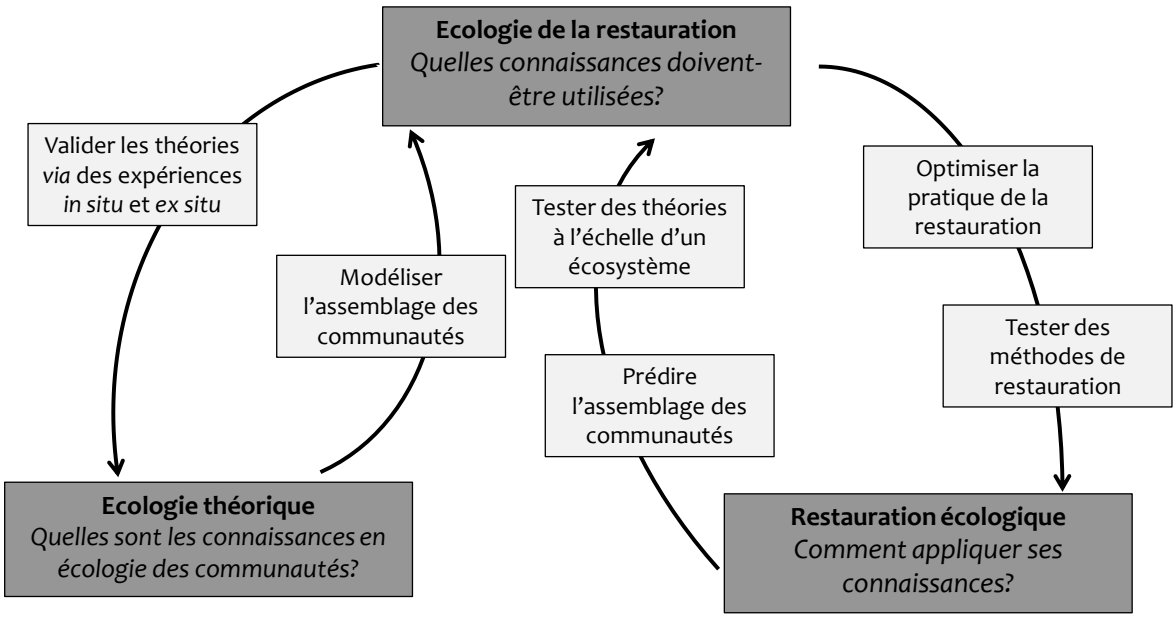


Figure I.3 : Relations entre l'écologie théorique, l'écologie de la restauration et la restauration écologique. Modifiée d'après Falk et al. (2006) et Jaunatre (2012).

I.4. L'écologie des communautés

I.4.1. Les communautés végétales

L'écologie des communautés étudie l'assemblage des espèces en terme de diversité, d'abondance et de composition dans une communauté ainsi que les processus et mécanismes de structuration à l'origine de ces assemblages (Vellend 2010). Parmi l'ensemble des définitions d'une communauté (Clements 1916; Gleason 1926; Clements 1936), « l'ensemble des individus de diverses espèces qui interagissent les unes avec les autres et avec les caractéristiques physiques de leur habitat » (Krebs 1972) synthétise les différentes approches du concept de communauté.

I.4.2. La succession

La succession végétale est décrite comme un changement progressif de la composition de la communauté dans le temps (Walker and Del Moral 2003). La succession primaire correspond à la colonisation d'un substrat vierge (e.g. coulée de lave, création d'île, Walker and Del Moral 2003) alors que la succession secondaire se développe sur un substrat préexistant, en présence d'une banque de graines et de

nutriments déjà dans le sol (e.g. rétablissement de la végétation après perturbation de feu ou abandon agricole, Mesléard et al. 1991; Mesléard and Lepart 1991; Hobbs and Cramer 2007).

Le premier modèle de succession (Clements 1916) décrit un mécanisme déterministe, où la communauté se développe d'un stade initial jusqu'à un stade climacique. Ce modèle, par ailleurs largement contesté, n'étant pas universellement applicable (Connell and Slatyer 1977) d'autres modèles fondés notamment sur l'importance de la stochasticité ont émergé. Les perturbations et tout événement stochastique introduisent de l'imprévisibilité dans le déroulement de la succession et les mécanismes de structuration de la communauté (Gleason 1926; Levin 1989; Young et al. 2001). Le modèle des états alternatifs stables (Sutherland 1974), intermédiaire entre le modèle déterministe et le modèle stochastique, sous-tend que les communautés, bien que structurées, sont susceptibles de se développer en de nombreux états alternatifs en raison de la part de hasard inhérente à tous les écosystèmes. Le développement de la communauté et sa succession sont ainsi expliqués à travers ces trois différents modèles qui permettent de prédire la trajectoire des communautés.

I.4.3. Perturbations, stress et résilience

Une perturbation, qu'elle soit naturelle ou le plus couramment anthropique, est un événement discret dans le temps qui modifie plus ou moins profondément la structure des écosystèmes, des communautés et des populations (White and Pickett 1985), fait varier les ressources disponibles et l'habitat physique, et bouleverse les relations de compétition (White and Jentsch 2001). La distinction entre perturbation et stress peut dans certaines situations poser problème, puisqu'un même événement peut être considéré comme stress ou perturbation selon l'échelle d'observation (Pickett et al. 1989). Un événement est considéré comme perturbation quand le seuil de tolérance d'un organisme pour un facteur donné est dépassé aboutissant à la mort ou au moins à une perte significative de biomasse (Grime 1977; Sousa 1984). L'effet d'une perturbation dépend donc de sa taille, de son intensité, de sa durée et de sa fréquence (Sousa 1984). La perturbation peut être soit exogène: l'événement provient de l'extérieur du système (e.g. exploitation minière) ; ou bien peut être considérée comme endogène : l'événement

de perturbation provient de l'intérieur du système ou du développement de la succession (e.g. une chute de l'arbre sénescent). Dans le cas d'un événement endogène continu (perturbation endogène non discrète, intrinsèque à l'écosystème) avec lequel l'écosystème évolue (e.g. pâturage), il pourra donc également être considéré comme un stress (McIntyre and Hobbs 1999).

Les notions de résilience et de résistance mesurent les impacts de la perturbation sur un écosystème ainsi que sa réponse. La résistance est définie par Mitchell et al. (2000) comme la capacité d'un écosystème à supporter une perturbation ou le niveau maximal de la perturbation que l'écosystème peut supporter sans changement significatif (***Figure I.4.A.***). La résilience est définie par Hirst et al. (2003) comme la capacité d'un écosystème à retourner à l'état précédant la perturbation (***Figure I.4.B.***).

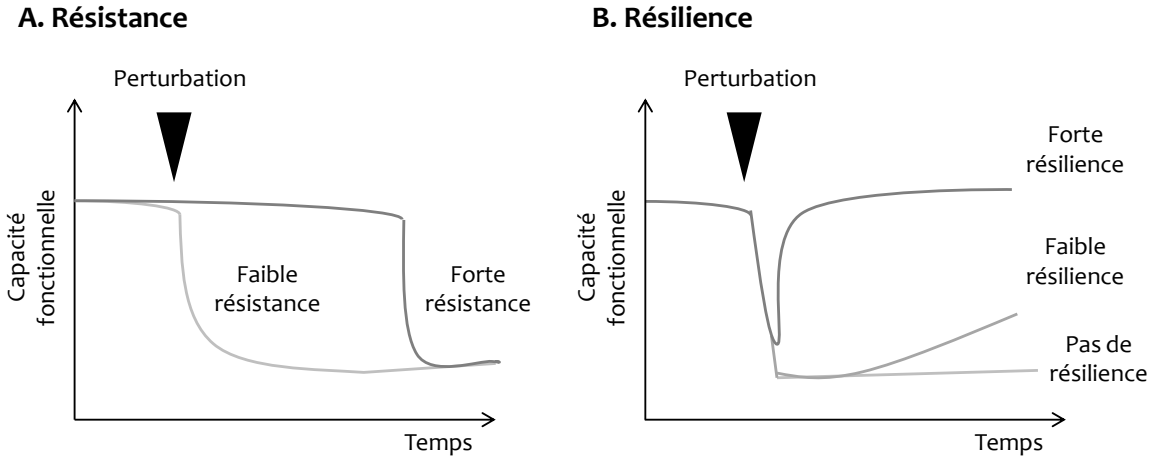


Figure I.4 : Représentation conceptuelle de la résistance (A) et de la résilience (B).

Les perturbations sont généralement considérées comme un facteur d'augmentation ou de maintien de la diversité; pour un milieu donné la richesse maximale est attendue pour un régime moyen de perturbation, empêchant ainsi les phénomènes d'exclusion d'espèces (Connell 1978). Cette théorie des perturbations intermédiaires est en partie controversée par des résultats empiriques et théoriques (Mackey and Currie 2001; Fox 2012). Malgré l'absence d'un modèle général, il est tout de même reconnu que les perturbations jouent un rôle majeur dans les mécanismes de succession des communautés végétales, et qu'elles doivent être identifiées lors de projets de restauration écologique. Le pâturage et l'assec, abordés dans cette thèse, sont

considérés comme des perturbations (Gibson and Brown 1992; Bonis 1998; Brock et al. 2003).

Le pâturage, en supprimant de la biomasse et en créant des microsites, peut modifier les interactions, limiter les effets de la compétition et favoriser le recrutement de nouvelles espèces ou individus (Lepš 1999; Bakker et al. 2006; Myers and Harms 2009). L'assec associé à une zone humide temporaire est un mécanisme puissant pour maintenir la diversité des espèces dans les communautés, en favorisant la coexistence d'un grand nombre d'espèces, via l'accumulation de stades de dormances d'espèces différents (Chesson and Warner 1981; Bonis et al. 1995; Chesson 2000).

De nombreux projets de restauration écologique concernent d'anciennes parcelles agricoles (Van der Putten et al. 2000; Hobbs and Cramer 2007; Prach et al. 2007; Cramer et al. 2008; Török et al. 2011b; Jírová et al. 2012). La mise en culture est aussi considérée comme une perturbation, mais à l'inverse des deux perturbations précédentes, les communautés végétales sont rarement adaptées aux impacts de l'agriculture après abandon: le labour et les amendements. L'absence de banque de graines des communautés avant culture (Hutchings and Booth 1996; Bossuyt and Honnay 2009) et des densités élevées d'espèces plus compétitrices, favorisées par les fertilisants (Marrs 2002; Standish et al. 2008) ont généralement un impact durable sur les communautés végétales.

I.4.4. Théories d'assemblage des communautés

Afin d'identifier les processus qui influencent la succession, des modèles d'assemblage des communautés ont été décrits. Le principal modèle utilisé est celui des filtres, proposé initialement pour les communautés d'invertébrés et de poissons (Southwood 1977; Poff 1997), puis modifié pour les communautés végétales (Keddy 1992; Fattorini and Halle 2004; Lortie et al. 2004; Guisan and Rahbek 2011). Ce modèle inclut un pool régional d'espèces, contraint par trois filtres (***Figure I.5***): le filtre de la dispersion, le filtre abiotique et le filtre biotique, qui sélectionnent les espèces de la communauté finale. Le filtre de la dispersion est souvent décrit comme un processus régional alors que les conditions abiotiques et les interactions biotiques sont considérées comme des processus internes (White and Jentsch 2004).

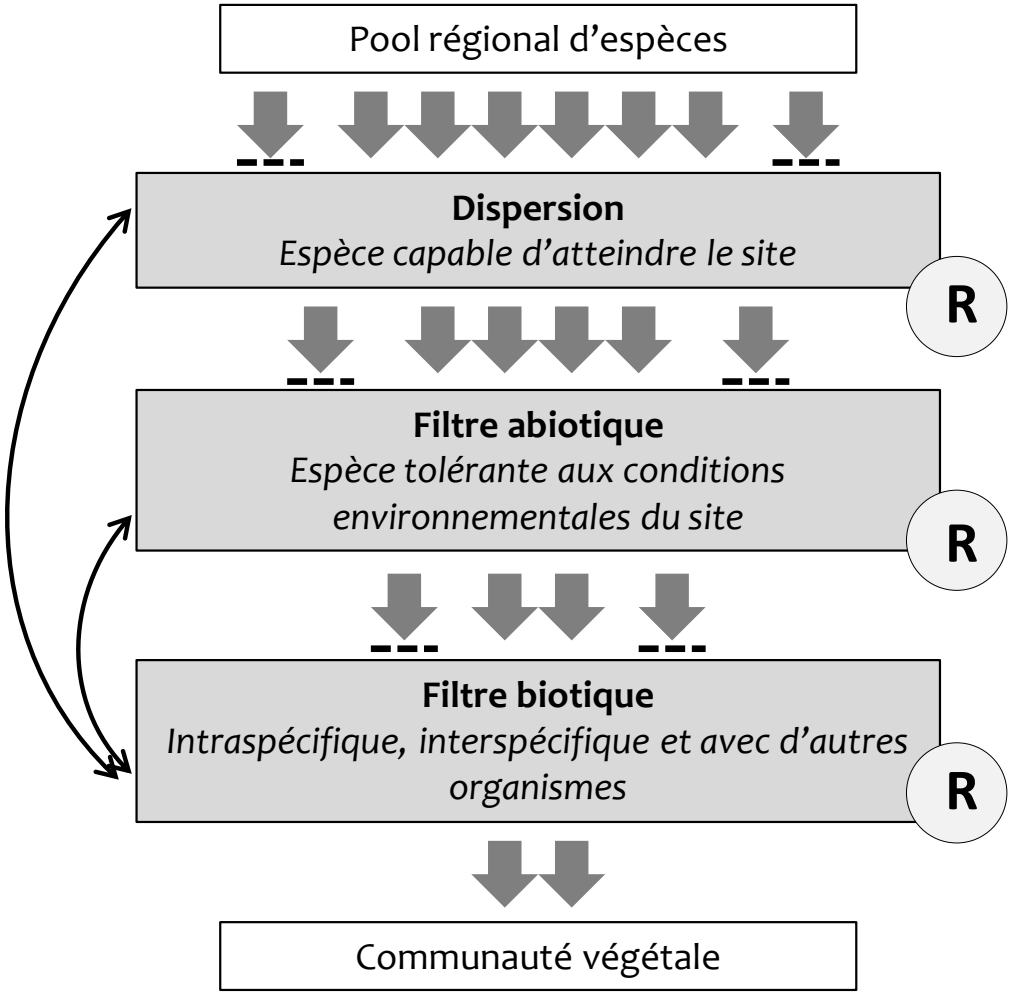


Figure I.5: Le modèle de filtre de l'assemblage des communautés. Les trois filtres sont représentés par les cases grises : la dispersion, le filtre abiotique et le filtre biotique. Les flèches grises représentent les espèces, capables ou non, de passer les filtres. Les boucles de rétroaction entre les filtres sont représentées par les flèches noires. Les disques « R » représentent les différents niveaux potentiels d'intervention de la restauration. Modifiée d'après Lortie et al. (2004) et Jaunatre (2012).

Le premier filtre est assuré par la dispersion : les espèces doivent être capables d'atteindre la communauté via le pool d'espèces externes (i.e. les espèces présentes dans le paysage qui se dispersent via la pluie de graines) ou via le pool d'espèces internes (i.e. les espèces présentes sur le site sous forme de banque de graines ou végétation établie). Les différents moyens de dispersion confèrent des capacités de dispersion spatio-temporelles variables selon les espèces leur permettant de franchir avec plus ou moins de succès le filtre de la dispersion.

Les conditions abiotiques opèrent un second filtre: les espèces doivent tolérer les conditions environnementales. L'ensemble des conditions physico-chimiques permettant à une espèce d'exister est localisé dans la niche écologique fondamentale (Grinnell 1917), prenant en compte les conditions nécessaires pour la germination, l'établissement et la reproduction de l'espèce (Grubb 1977).

Lorsqu'une espèce du pool régional parvient à franchir le filtre de la dispersion et n'est pas contraint par le filtre abiotique, son devenir dans la communauté est déterminé par le filtre biotique, i.e. les interactions avec les individus de la même espèce (intraspécifique) ou d'autres espèces (interspécifique), ou avec d'autres organismes au sein de l'écosystème (e.g. les herbivores). Les interactions peuvent avoir un effet négatif (e.g. compétition) ou positif (e.g. facilitation) sur l'installation et/ou la croissance des individus (Callaway and Walker 1997; Bruno et al. 2003). La compétition naît de la concurrence entre individus ou espèces pour une même ressource limitée (e.g. eau, lumière, nutriments, espace, pollinisateurs ; Naeem et al. 1999), entraînant une modification, pour l'ensemble ou une partie des individus ou espèces, de la survie, la croissance et/ou la reproduction (Grime 1973). La facilitation, au contraire, par l'amélioration d'un ou plusieurs facteurs du milieu, augmente la survie, la croissance et/ou de la reproduction d'un individu ou d'une espèce permettant son installation et/ou son maintien au sein d'une communauté (Connell and Slatyer 1977; Glenn-Lewin et al. 1992). La compétition a longtemps été considérée comme l'interaction majeur dans l'assemblage des communautés, pour autant les interactions positives jouent également un rôle significatif (Maestre and Cortina 2004; Callaway 2007; Brooker et al. 2008).

Les communautés évoluant au fils du temps, les filtres sont dynamiques et dépendants entre eux (boucle de retroaction: ***Figure I.5***, Fattorini and Halle 2004).

L'identification des rôles respectifs des filtres et leur manipulation lors d'opérations de restauration (***Figure I.5***) permettent de faciliter la colonisation des espèces cibles. La dispersion (et la limitation en recrutement de graines) a ainsi souvent été identifiée comme un facteur plus important dans l'assemblage des communautés que les processus internes (e.g. prédation, compétition, facilitation ; Niering and Goodwin 1974; Palmer et al. 1996; Turnbull et al. 2000; Mouquet et al. 2004; Clark et al. 2007). Les modèles de

dispersion divergent, en considérant la sélection des espèces au sein de la communauté comme stochastique (le modèle de loterie ; Chesson and Warner 1981; Chesson 1991) ou au contraire en privilégiant les capacités de dispersions des espèces et la distance à parcourir pour atteindre la communauté donnée (modèle de la biogéographie insulaire ; MacArthur and Wilson 1967). Les processus internes interviennent alors dans un second temps et sont largement tributaire de la dispersion. Des études récentes montrent cependant que les processus internes peuvent très largement déterminer la composition de la communauté, la présence ou l'absence de certaines espèces pouvant être attribuées aux interactions biotiques et non à la dispersion (Mouquet et al. 2004; Münzbergová and Herben 2005; Myers and Harms 2009; Klimkowska et al. 2010b). La hiérarchisation de l'importance des filtres dans l'assemblage des communautés dépend donc du contexte, les filtres étant dynamiques, ils interviennent d'autre part avec différentes intensités aux différents stades de développement de la communauté végétale (Keddy 1992; Hobbs and Norton 2004).

Le concept de filtre exprime une vision déterministe des mécanismes de structuration des communautés végétales, dans laquelle le résultat est hautement prévisible et les mécanismes de succession manipulables, permettant d'atteindre la communauté de référence (Luken 1990). Récemment, les partisans des théories neutres ont mis l'accent sur l'importance des facteurs stochastiques et historiques, préconisant une approche plus complexe de l'assemblage des communautés (Chase 2003; Chave 2004; Tilman 2004; Hubbell 2005; Chase 2007; Jabot et al. 2008). La composition d'une communauté peut en effet être fortement influencée par des facteurs historiques (Drake 1990; Chase 2003) et des communautés sur des sites présentant de fortes similitudes peuvent diverger à la suite d'événements différents. C'est par exemple le cas des effets de priorités dans lesquels l'ordre de colonisation des espèces influence la composition de la communauté finale (Drake 1990; Trowbridge 2007; Kardol et al. 2013) et où la stochasticité joue un rôle prépondérant dans la séquence d'arrivée des espèces (i.e. notamment la première arrivée). Ces deux types de modèles (déterministe *vs.* stochastique) considérés conjointement sont des outils précieux en restauration (Suding et al. 2004; Collinge and Ray 2009; Török et al. 2011b; Fukami and Nakajima 2011), car ils permettent notamment l'intérêt de manipuler le filtre de la dispersion.

I.4.5. Des théories d'écologie à la pratique de la restauration écologique

Le défi de la restauration des communautés végétales est de comprendre et d'exploiter les mécanismes de la succession écologique à tous les stades de développement, en accélérant, complétant ou contournant les processus de colonisation naturels (Keesing and Wratten 1998). Les filtres dans le contexte de la restauration peuvent être assimilés à des leviers (***Figure I.6***, Whisenant 1999), manipulés pour franchir des seuils et atteindre la trajectoire de référence. Ces trois leviers de restauration ont ainsi été utilisés en restauration: dispersion (Kiehl et al. 2010), filtre abiotique (Bobbink et al. 1998; Verhagen et al. 2001) ou filtre biotique (Padilla and Pugnaire 2006; Pywell et al. 2007; Collinge and Ray 2009).

Un panel d'actions diverses peut être utilisé pour modifier la trajectoire de la communauté (***Figure I.6***). L'introduction de propagules d'espèces cibles permet de contrecarrer le filtre de la dispersion. Néanmoins les introductions de propagules doivent se faire après restauration des conditions abiotiques, afin d'éviter des phénomènes similaires aux effets de masse spatiale (Spatial mass effect: une espèce peut se trouver dans un habitat défavorable, où elle ne peut se régénérer, en raison d'un flux de propagules d'une source existante dans un habitat favorable à proximité; Shmida and Ellner 1985; Zonneveld 1995; Zelenỳ et al. 2010) où les propagules ou individus transférés ne rencontrent pas des conditions abiotiques favorables. Les premières interventions d'un projet de restauration doivent donc viser à se rapprocher des conditions abiotiques de l'écosystème de référence (e.g. restauration du régime hydrique, réduction des excès de nutriments dans le sol, etc.). Favoriser le développement d'espèces structurantes peut aussi faciliter et améliorer la colonisation par des espèces cibles (i.e. utilisation des effets de priorités; Tirado and Pugnaire 2005; Trowbridge 2007; Collinge and Ray 2009; Kardol et al. 2013).

Dans cette thèse, le ***chapitre 2*** concerne cette manipulation du filtre abiotique sur les communautés végétales, les ***chapitre 3.1*** et ***chapitre 4*** traitent de l'effet de la manipulation du filtre de la dispersion en addition de la manipulation du filtre abiotique, par l'introduction des espèces des communautés végétales de référence selon deux méthodes, le transfert de foin et le transfert de sol. Le ***chapitre 3.2*** concerne l'effet du transfert de sol sur les communautés d'invertébrés aquatiques.

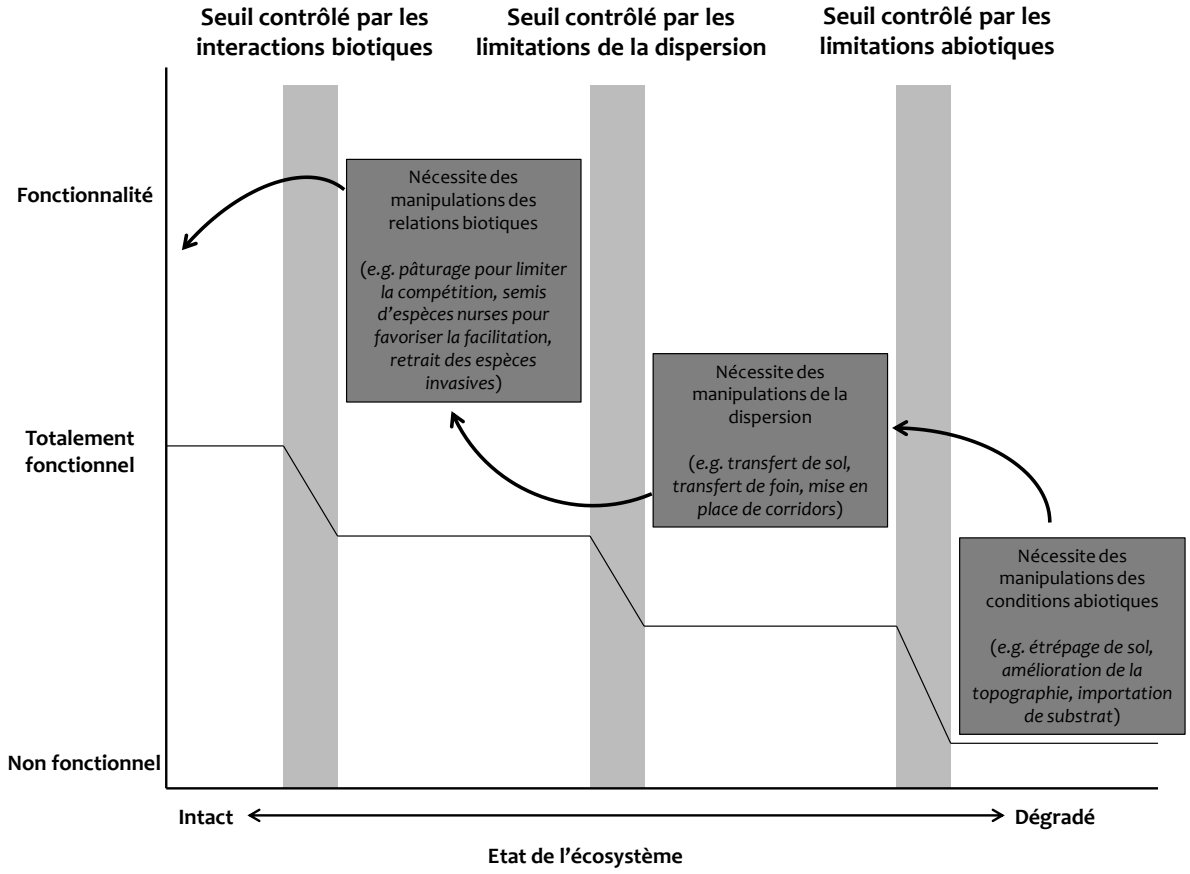


Figure I.6: Modèle de transition d'un écosystème entre différents états de fonctionnalité, illustrant la présence de trois types de seuil : un premier contrôlé par les limitations biotiques, un second contrôlé par les limitations de la dispersion, et un troisième contrôlé par les interactions biotiques (modifié de Whisenant 1999). Des exemples de méthodes utilisées en restauration pour dépasser les seuils à l'installation de la communauté de référence (i.e. écosystème intact) sont inscrits en parenthèse et en italique.

I.5. Evaluation de la réussite d'une restauration

I.5.1. Les indicateurs

La restauration écologique vise à restaurer l'écosystème dans son intégrité et cherche donc à rétablir la biodiversité et l'ensemble des fonctions de l'écosystème. Cette restauration de l'ensemble des compartiments et fonctions dépend entre autre, des mécanismes successionnels, son succès ne peut être appréhendé qu'à moyen ou long terme nécessitant la définition d'indicateurs précis, la mise en place et la poursuite de leur suivi. Le choix des indicateurs est fonction des objectifs fixés; ils permettront une

approche d'autant plus globale qu'ils intègreront un maximum de compartiments de la diversité biologique (Choi 2007; Cristofoli and Mahy 2010). Cependant, les budgets consacrés aux suivis sont très généralement sous estimés voire inexistants (Cristofoli and Mahy 2010). Développer des mesures faciles à réaliser et peu coûteuses correspond donc à une démarche particulièrement pertinente. Ces mesures privilégient souvent les communautés végétales, qui sont généralement un compartiment visé dans les projets de restauration et qui ont un rôle structurant des écosystèmes. Classiquement, l'évaluation d'une restauration repose sur une approche espèce (e.g espèces en danger, espèces patrimoniales) mais n'apporte qu'une information restreinte par rapport aux divers compartiments de l'écosystème. Ainsi se focaliser sur la globalité de la communauté végétale semble un choix plus judicieux, même la prise en compte de la communauté ne suffit pas à caractériser la globalité de l'écosystème.

I.5.2. L'approche communauté végétale

La richesse spécifique est l'un des indicateurs les plus couramment utilisé susceptible d'exprimer certaines fonctionnalités de l'écosystème, dans la mesure où une richesse spécifique plus élevée faciliterait le bon fonctionnement et la stabilité des écosystèmes (Ehrenfeld and Toth 1997; Hooper et al. 2005; Tilman et al. 2006), leur permettant de répondre aux perturbations et d'éviter les invasions (May 1973; Hobbs et al. 1995; Tilman 1997). Néanmoins la pertinence de cet indicateur paraît discutable si l'on considère le rôle joué par les espèces clés ou ingénieurs (Brown 1995; Jones and Lawton 1995; Stone 1995; Naeem et al. 1996; Grime 1998; Bakker et al. 2000 ; abordées en ***Discussion*** avec les effets de priorités), et la richesse spécifique ne peut être le seul critère de restauration pris en compte dans un projet de restauration (Ilmonen et al. 2013). Ainsi, au lieu d'être considérée dans son ensemble (nombre total d'espèces), la richesse spécifique peut être décomposée en espèces cibles présentes dans les communautés de référence et espèces non cibles, complétées par divers indices, notamment de similarité avec les communautés de référence (i.e. indice de Sorensen, indice de Bray-Curtis). Ces différents indicateurs ont ainsi été utilisés afin d'évaluer les techniques de restauration mises en place (***chapitre 3.1*** et ***chapitre 4***). Afin de mettre en avant les espèces sous ou sur-représentées dans les communautés restaurées, nous avons testé deux nouveaux indicateurs,

complémentaires, (Jaunatre et al. 2013b, ***Annexe 1***) prenant en compte la diversité, la composition et la structure de la communauté par rapport à la communauté de référence.

I.5.3. Prise en compte d'autres compartiments de l'écosystème

La prise en compte de divers compartiments de l'écosystème permet une approche globale de l'évaluation de la restauration. Les communautés animales étant le plus souvent liées aux à la nature et la structure des communautés végétales (Luken 1990; Duelli and Obrist 2003), la faune est potentiellement un indicateur de la qualité de et du niveau de restauration de l'écosystème (Palmer et al. 1996; Kiehl and Wagner 2006; Cristescu et al. 2013). L'intégration d'une composante faunistique réalisée dans le ***chapitre 3.2*** permet de considérer certaines fonctions du système, peu ou non prise en compte en prenant des critères exclusivement végétaux.

I.6. Caractéristiques de la Camargue

I.6.1. Contexte géographique et géologique permettant une diversité de milieux

La Camargue, situé au Sud de la France (***Figure I.7***) est une vaste plaine alluviale de 150 000 hectares. Le delta du Rhône est le plus grand de l'Europe de l'Ouest, limité à l'Est par la plaine de la Crau et à l'ouest par la costière du Gard. Les deux bras du Rhône compartimentent la Camargue en trois secteurs : le secteur occidental ou « Petite Camargue », le secteur central ou « Grande Camargue » et le secteur oriental ou « Plan du Bourg » (***Figure I.7***). D'un point de vue géomorphologique et biologique, ces trois secteurs forment un même ensemble. La Camargue est le résultat du combat permanent entre les eaux du Rhône chargées d'alluvions et la mer Méditerranée. La formation du delta du Rhône et sa perpétuelle évolution au cours des siècles ont façonné un paysage spécifique, caractérisé par l'absence de relief important. Cependant, les micro-variations de ce relief, liées à la complexité des dépôts salés ou doux, engendrent des changements importants dans le régime de l'eau et du sel, qui induisent l'imbrication des milieux naturels, composés en « mosaïque ». Cette mosaïque d'habitats, conditionnée par l'eau, le sel et la topographie, est à l'origine du grand intérêt de la Camargue en ce qui concerne la

faune et la flore. A cela, il faut ajouter l'influence du climat méditerranéen, notamment une évapotranspiration importante (liée à de forts vents et des températures élevées, 1200mm/an, Heurteaux 1970) et une faible pluviométrie (550m/an, Heurteaux 1976), qui agit de façon sensible sur l'évolution du paysage et de l'habitat.

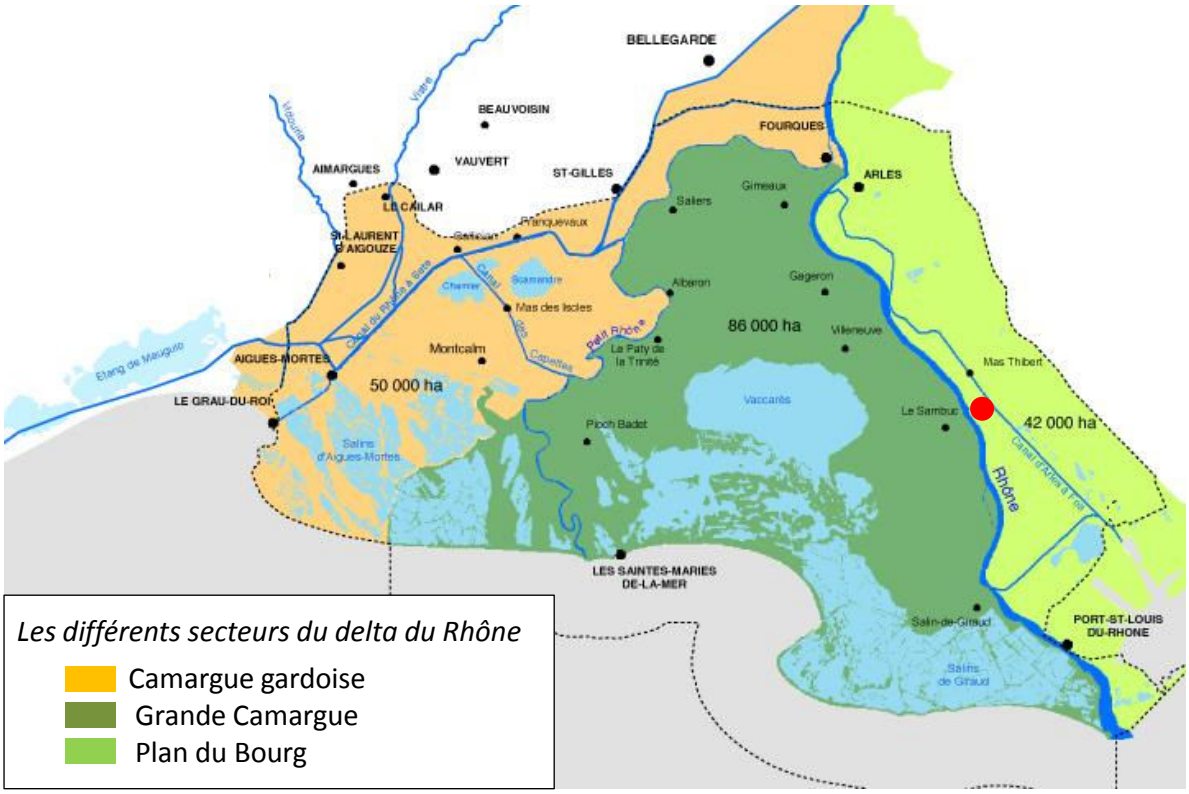


Figure 1.7: Les différents secteurs de la Camargue. Le point rouge représente le domaine du Cassaïre.

I.6.2. Un delta : son histoire et sa dynamique en lien avec une diversité d'acteurs

Les activités humaines en Camargue, qui ont connu de profonds changements, se sont fortement accrues au 19ème siècle, le développement des machines et des énergies vapeurs puis fossiles facilitant le développement des activités et de leurs impacts sur le milieu naturel. L'endiguement et la maîtrise du débit du Rhône dès la première moitié du 19ème siècle, font de son delta un espace fortement artificialisé. La Camargue est un hydrosystème complexe (Chauvelon et al. 2003), où l'eau douce du Rhône est pompée dans la plaine deltaïque via un réseau de canaux d'irrigation pour dessaler les champs à des fins agricoles (principalement pour la culture du riz inondé) et pour la gestion des marais. Outre la culture du riz, l'industrie et le tourisme ont conduit depuis la seconde

guerre mondiale à une perte de 40 000 hectares d'espaces naturels (Tamisier 1991). Malgré toutes ces activités, la Camargue abrite une grande biodiversité, dont 75 espèces de poissons, 10 espèces d'amphibiens, 15 espèces de reptiles, 400 espèces d'oiseaux et plus de 1000 espèces végétales, dont de nombreuses espèces endémiques et menacées (Tour du Valat 2000). D'actuels changements d'occupation du sol peuvent être des opportunités pour restaurer des écosystèmes dégradés par les activités agricoles. C'est notamment le cas du domaine du Cassaïre, situé à l'est du grand Rhône (***Figure I.7***), projet participatif de restauration présenté dans le ***Chapitre 1***.

Transition to Chapter 1

The first objective of a restoration project is to determine the reference ecosystem, which describes what the ecosystem should be like after restoration (Clewell and Aronson 2007). The choices of restoration objectives are determined by historical considerations, ecological values, social acceptance, economics and political constraints (Bullock et al. 2011). Our reference ecosystem, based on social participatory project, ecological values and historical ecology, is determined and discussed in ***Chapter 1***.

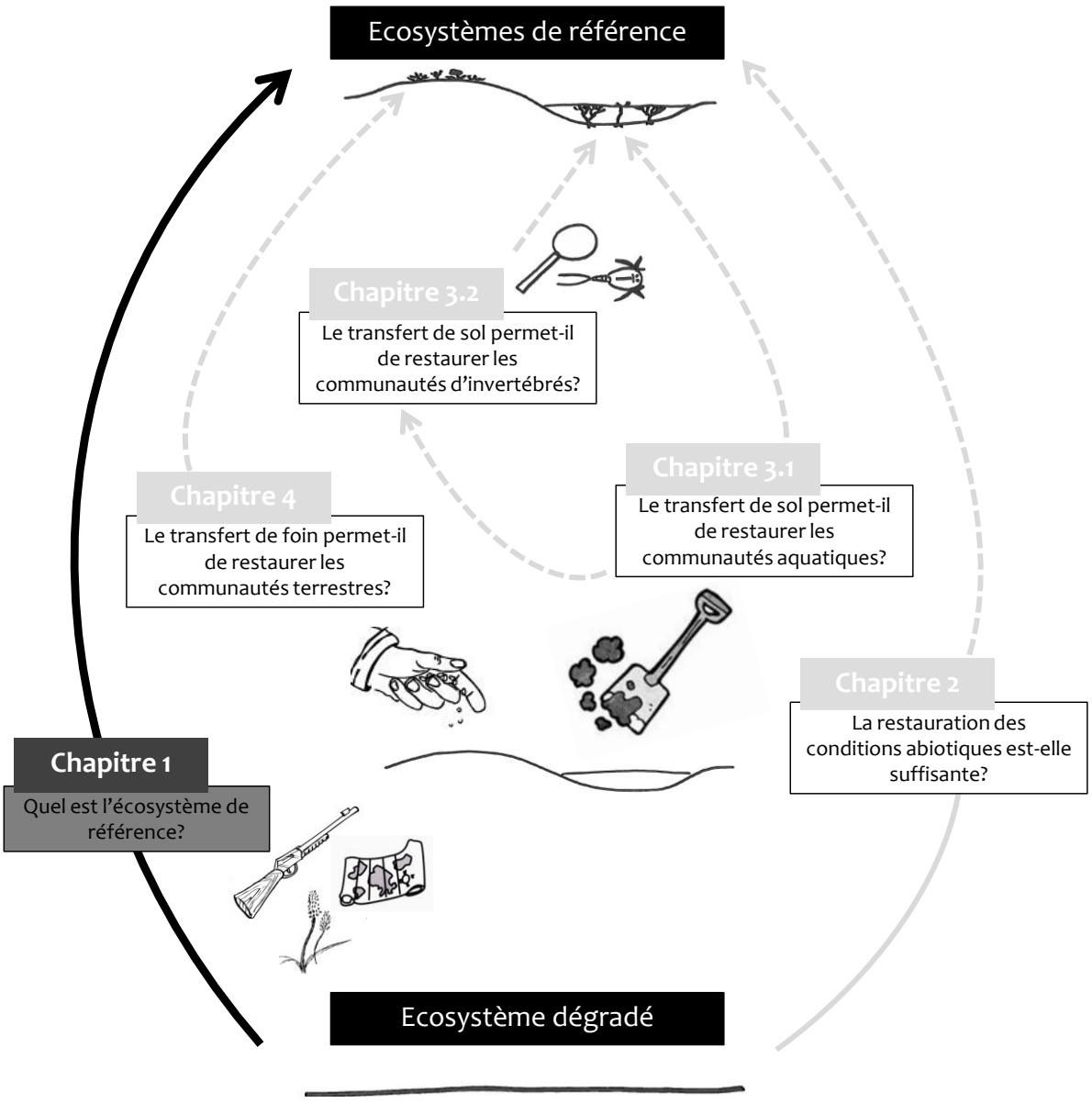


Figure T1.1: Location of ***Chapter 1*** in the general thesis organization

The Mediterranean meso-xeric grassland plant community (*Bellis annua* spring flowering).

The Mediterranean temporary wetland plant community (*Ranunculus peltatus*).
Photo credit: Simon Baudouin

Chapter 1 - Presentation of the Cassaïre restoration project and goals

With the collaboration of Johan Friry

1.1. Defining reference ecosystem

Sensu stricto, restoration refers to returning an ecosystem to an undisturbed or historical state, despite the fact that today, a broader set of activities define ecological restoration *sensu lato*, such as the creation of ecosystems where they did not previously exist (Palmer 2009). In both cases, defining the restoration reference is an essential step because it allows practitioners to set restoration objectives, to guide the restoration process and to assess success (Society for Ecological Restoration 2004; Clewell and Aronson 2007; Miller and Hobbs 2007). Besides identifying the reference ecosystem, the disturbances to the ecosystem to be restored have to be identified and their effects understood (Hobbs and Norton 1996; White and Jentsch 2004; Hobbs and Cramer 2007). In addition, the resilience of the ecosystem to be restored has to be studied (Mitchell et al. 2000; Hirst et al. 2003). The reference can be defined in different ways: 1) it can correspond to the historical ecosystem; 2) it can be defined to solve environmental issues, for example to restore some ecosystem services or 3) it can correspond to a socio-ecosystem.

The historical ecosystem corresponds to the ecosystem before a severe anthropogenic disturbance (e.g. intensive cultivation). This form of reference was used by Aldo Leopold in the first restoration projects in the 1930s in the United States to remedy land-abandonment and aid soil conservation in the prairies of Wisconsin. In speaking about reference, Aldo Leopold remarked: "Our idea is to reconstruct a sample of original Wisconsin, a sample of what Dane County looked like when our ancestors arrived here during the 1840s" (Leopold 1999). Using the pre-disturbance state to guide restoration can be useful if enough is known of the historical conditions and if large areas of the pre-disturbance state are still found in the landscape; however aiming for ecosystems, that precisely replicate the past and that are no more sustainable in the actual context, is a practice that is unlikely to deliver self-sustaining results (Choi 2007).

A reference defined to solve environmental issues corresponds more to ecological engineering or to reclamation than to ecological restoration *sensu stricto*. The "*Restauration des Terrains en Montagne*" (Mountain Ecosystem Restoration) agency has been carrying out this type of restoration since 1860 in France, principally by reforesting degraded pastures to prevent soil erosion (Combes 1989). Within this paradigm,

ecological values (e.g. species or habitat with conservation value, biodiversity, or potential habitat for rare, endemic and/or threatened species) are taken less into account and serve as a means to solving technical problems related to human activities.

When historical ecosystems are difficult to define or when using them is unrealistic in a context of climate changes and fragmented landscapes (Millar and Brubaker 2006), another reference ecosystem must be defined (Jackson and Hobbs 2009). Recently, reference ecosystems have been determined with regard to both ecological values and social issues (Choi 2007; Clewell and Aronson 2007; Moreno-Mateos and Comin 2010). These socio-ecosystems consist of a collective construction of integrated, complex and adaptive systems, coupling nature and human societies, with the Human considered as an active component of the ecosystem, and with an integrated approach to human-nature interactions. Under these conditions, the final choice of reference is unavoidably subjective and arbitrary (Choi 2004), but it leads to public acceptance and a higher probability of restoration success (Gobster and Hull 2000). While ecological constraints define what is possible and financial constraints determine what is realistic, social constraints determine whether a given restoration project is acceptable (Miller and Hobbs 2007) and whether it matches local social needs. In such reference ecosystems, successful restoration must be predicated on the communication of project goals and benefits to humans, and on consultations along with open dialogue to evaluate public understanding, acceptance, and support (Miller and Hobbs 2007).

1.2. The Cassaïre project

1.2.1. Restoration project at the Cassaïre site

In a delta as modified by human activity as the Camargue area, where local stakeholders are deeply involved in the management of the environment, reflections around a socio-ecosystem for a restoration project make sense. Moreover, on such a basis, defining a natural state is not straightforward and may not even be appropriate: is the natural state the condition that existed before cultivation or is it the condition that would exist in the absence of all human influences (e.g containment of the Rhône river)? Considering a reference ecosystem based on conservation objectives linked with the

current landscape and local demand seems to be the best way to have a successful restoration project. This is the case with the Cassaïre restoration project located east of the Camargue area (43°31'N, 4°44''E, Plan du Bourg, Rhône delta, Southern France, ***Figure 1.1***).

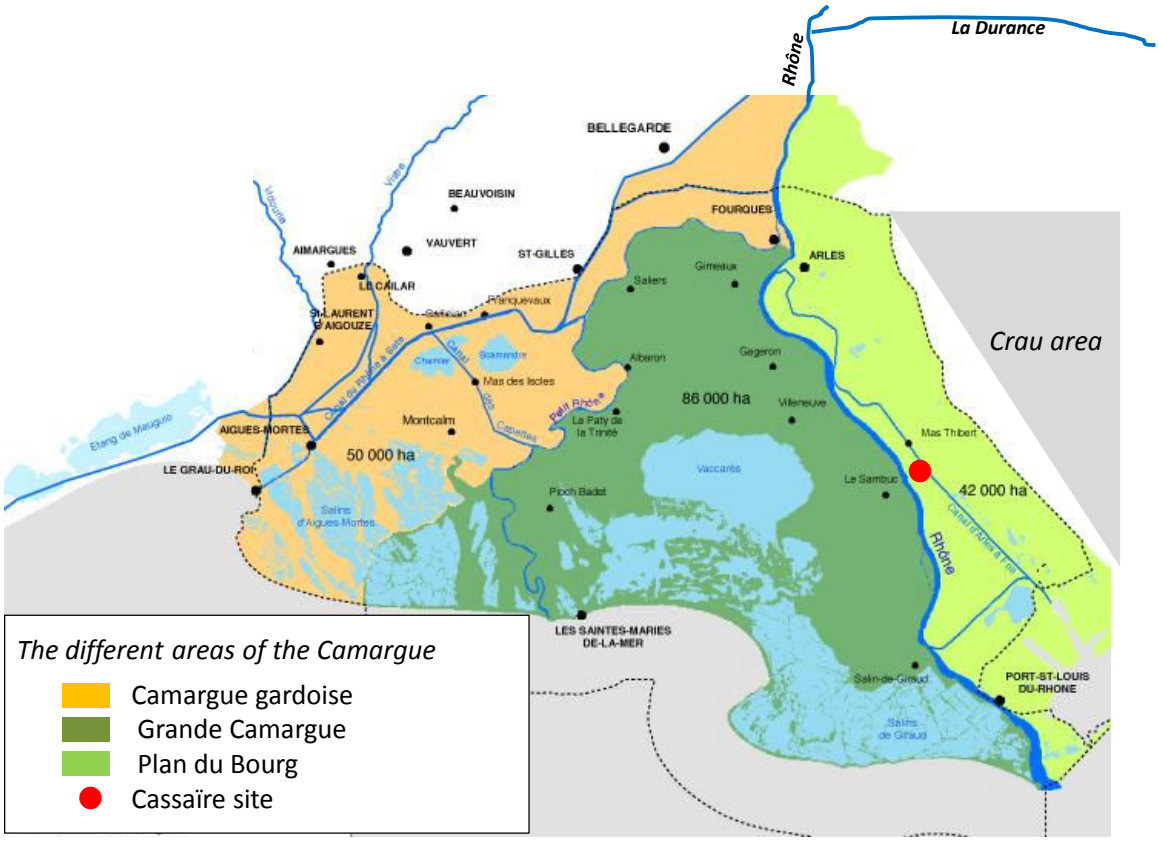


Figure 1.1: The different areas of the Camargue and the location of the Cassaïre site (red dot) in the Plan du Bourg area. The Durance river, the Rhône, and the Crau area, are also shown. Figure adapted from the official Regional Park of the Camargue area map.

Covering more than 70 hectares, the Cassaïre site is composed of a mosaic of habitats, a majority of fallow land which have been heavily transformed by humans through cultivation-related activities (such as leveling, grading, drainage, irrigation, and amendment). The remaining relic natural habitats (comprising a grand total of less than 7 hectares) correspond to the following three priority habitats according to the Natura 2000 Network of the European Union Habitat Directive (European Commission 1992): fluvial dunes linked to Rhône sand deposit, meso-xeric grasslands on the highest parts of the site, and salt marshes on the lower parts (***Figure 1.2***).

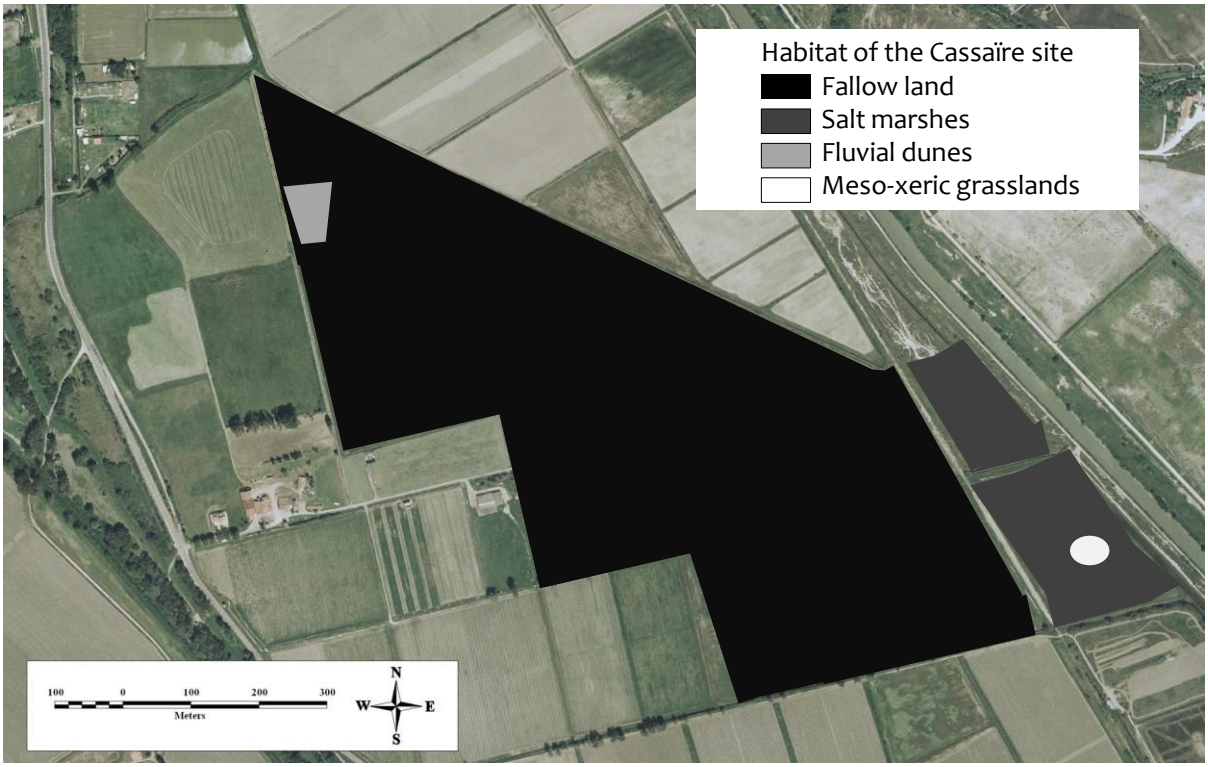


Figure 1.2: Habitat map of the Cassaïre site, with a majority of fallow land (in black) and remaining relictual natural habitats (the meso-xeric grasslands in white, the dunes in light grey and the salt marshes in dark grey).

In 2004, after farming cessation, the site was acquired by Conservatoire du Littoral et des Rivages lacustres (a state conservancy agency) and its management was entrusted to an NGO "Les Amis des Marais du Vigueirat", which now administrates the surrounding National Nature Reserve "les Marais du Vigueirat". Although the entire project was completely financed by L'Agence de l'Eau (the Water Agency), Conseil Régional Provence-Alpes-Côte-d'Azur (the Regional Council), and Conseil Général des Bouches-du-Rhône (the Departmental Council), all design and implementation decisions were taken collectively by a steering committee composed of the following stakeholders:

1) Environmental managers: the National Reserve managers of Les Amis des Marais du Vigueirat (NGO which administrates the National Nature Reserve), the Parc Naturel Régional de Camargue (the Natural Regional Park of the Camargue), and the Office National de la Chasse et de la Faune Sauvage (the National Office for Hunting and Wildlife).

2) Project managers and funders: Le Conservatoire du Littoral et des Rivages lacustres (a state conservancy agency), L'Agence de l'Eau (the Water Agency), Le Conseil Régional Provence-Alpes-Côte-d'Azur (the Regional Council), and Le Conseil Général des Bouches-du-Rhône (the Departmental Council).
3) Local stakeholders: The hunting association of Mas Thibert hamlet and the Departmental hunting federation
4) Scientists, experts, and researchers from the Tour du Valat (Research center dor conservation of Mediterranean wetlands), and the Mediterranean Institute of Biodiversity and Ecology (IMBE).

Even when the various stakeholders did not share the same expectations, the various meetings and steering committees resulted in a consensus. It was ultimately decided that the restoration project be developed for sustainable and harmonious development in connection with the neighboring hamlet hunters. The objective of this project is twofold: creating, for conservation value, complementary habitats from those present on the Vigueirat National Nature Reserve, and achieving this while allowing some hunting activity to continue as negotiated with local community stakeholders. Indeed, in the Camargue area, traditional rural activities, especially hunting, are important. Creating a wetland would increase the size of the available hunting ground for town hunters, who do not currently have much. Moreover, it would induce a close collaboration between nature reserve managers and hunters who have drastically different ways of managing wetland hydrology (hunters keep standing water in summer to attract waterfowl, leading to hydrological functioning in contrast to Mediterranean temporary wetlands, whose management has resulted in severe consequences for biodiversity see also ***1.2.2.1 Mediterranean temporary wetland***). Because funding for a project can depend on its level of public acceptance (Miller and Hobbs 2007), local participation is an essential ingredient for project success. The conflicts and compatibilities of the Cassaïre restoration project objectives were carefully considered, and the project now stands out as a shining example of co-management that properly takes into account local acceptance, projected benefit, social, financial, and ecological goals and constraints (***Figure 1.3***).

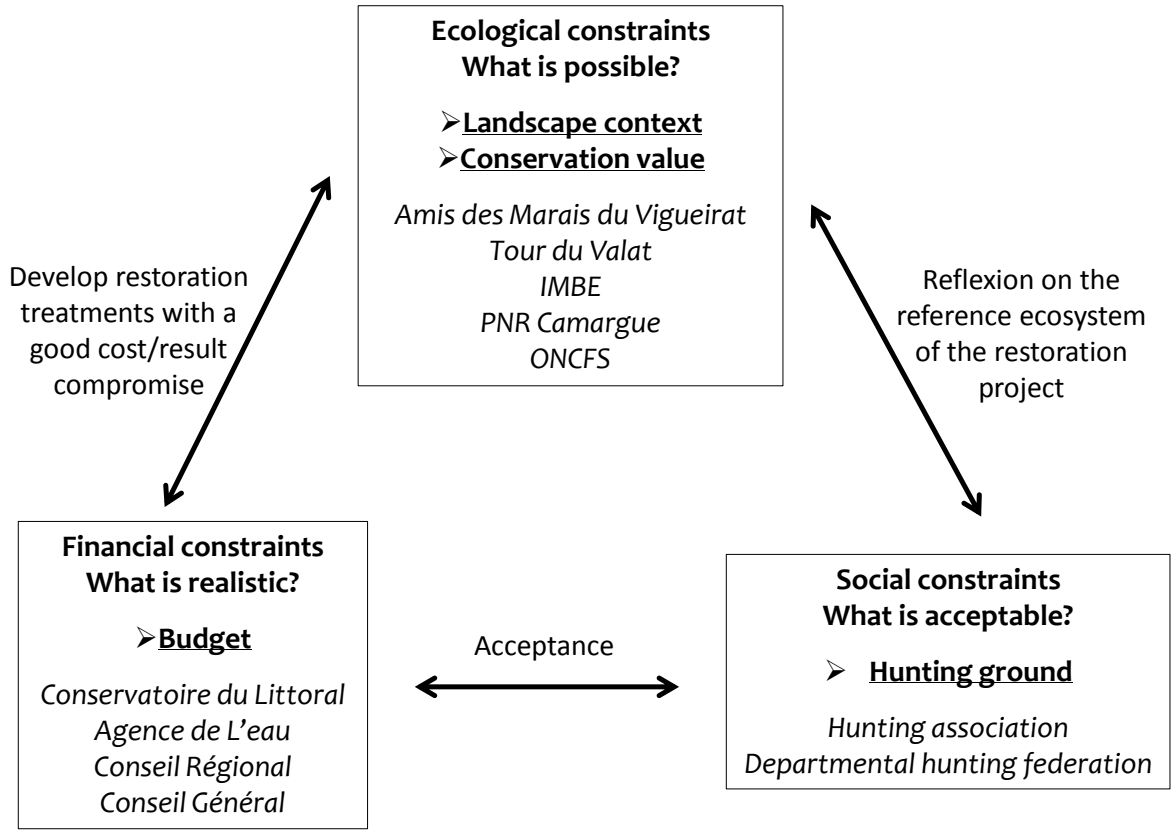


Figure 1.3: Conceptual organization chart of the project design. Figure modified from Miller and Hobbs (2007).

As determined by Donadieu (2002), the reference selection process needs to address the following four questions: 1) From whom to restore?, 2) What to restore?, 3) How to restore? and 4) How to evaluate the long-term success of the operation?

For the Cassaïre site, the answers to these questions were: 1) for biodiversity and for the hunters, 2) a Mediterranean temporary wetland with high conservation value and suitable for hunting activities, 3) by using advanced engineering techniques, and 4) by using the notion of target species. Indeed, even though the facilitation of hunting activities was a major objective, the primary aim was to create natural habitats similar to the high conservation value habitats found in Camargue, and complementary to those of the Vigueirat National Nature Reserve. The notion of target species is thereby directly linked to the concept of reference ecosystems. These species are the species present in the reference and are usually contrasted with non-target species which are species absent from the reference. A reduction in the number of non-target species accompanied by an increase in the number of target species can be an objective and an indicator of

success in a restoration project (used in ***Chapter 2***, ***Chapter 3*** and ***Chapter 4***), though it must be used with caution (Davis et al. 2011). A index was thereby developed using target and non-target abundances, indicating whether the target community objective was reached (***Annexe 1***, Jaunatre et al. 2013b). Because the restoration project incorporated local stakeholders, other evaluation guidelines, which include social components, could be used as success indicators (such as the support of local stakeholders, hunting tables, and ecosystem services) and are proposed in the ***General Discussion***.

1.2.2. Reference ecosystems of the Cassaïre site

1.2.2.1. Mediterranean temporary wetland

Mediterranean temporary wetlands are depressions, characterized by variable floodings (concentrated in autumn, winter and spring) and a summer dry-out (Grillas et al. 2004). They represent one of the most remarkable Mediterranean habitats, comprising a high plant diversity with many annual species, some of which are rare and endangered. These plants are well adapted to the Mediterranean climate because, by being annual they, are able make it through the dry summer and take advantage of the short favorable periods for reproduction. Examples include *Zannichellia obtusifolia* Talavera & al., *Callitriche lenisulca* Clavaud or *Tolypella hispanica* C.F.O. Nordstedt ex T.F.Allen (Grillas and Duncan 1986; Grillas et al. 2004). Grazing helps to keep the habitat open and to aerate the soil by trampling. These habitats have lost their identity with the work of hydraulic facilities (containment and supply of fresh water) and have been subjected in recent decades to degradation and drastic area reduction due to agriculture, industry, recreational activities, and hunting (Hollis 1992; Grillas et al. 2004), making this type of habitat rare (***Figure 1.4***). Indeed, one of the main causes of degradation in Mediterranean temporary wetlands is water management in support of hunting activities in which water levels are maintained in summer, to attract waterfowl, and this has gradually favored perennial and cosmopolitan species over plant communities that are restricted to temporary wetlands (Tamisier and Grillas 1994; Aznar et al. 2003). The artificial addition of freshwater in summer is contrary to the natural functioning of wetlands and leads to conflicts and strong contention between conservationists and hunters, a recurrent issue

that has been demonstrated yet again in a recent county hunting journal article that is critical of nature reserve managers (Chauvet 2012).

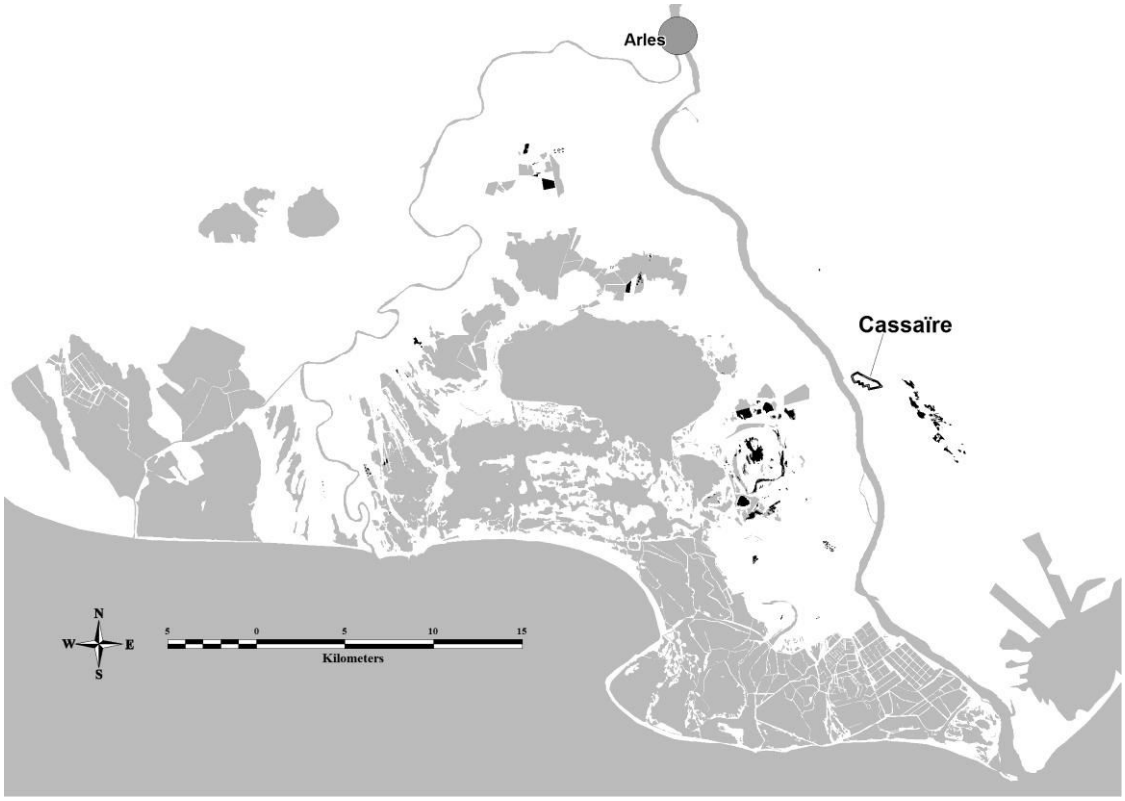


Figure 1.4: Distribution of the Mediterranean temporary wetlands (in black) in Camargue area and location of the Cassaïre site. The grey shading indicates the other wetland types in the Camargue area.

1.2.2.2. Mediterranean meso-xeric grassland

Mediterranean temporary wetlands are found in a mosaic together with many other habitats, including Mediterranean meso-xeric grasslands. It was therefore decided that a topography favorable to meso-xeric grasslands be created in addition to the depressions needed for temporary wetland restoration. A convenient way of simultaneously restoring both habitats is to use the soil that is removed, in creating the depressions, for establishing restored grassland. Meso-xeric grassland is already present on the Cassaïre site as relics of natural habitats (***Figure 1.2***). Such grassland is found on never-flooded old eroded dune relief (fluvial or marine) that is less subject to the influence of salt than lower areas. This habitat has the highest plant richness in the Camargue area (Molinier and Tallon 1970; Braun-Blanquet 1973), composed in high proportion of annual species, such as *Brachypodium distachyon* (L.) P. Beauv., *Galium murale* (L.) All., or *Scorpiurus*

muricatus L.. These grasslands are traditionally managed by extensive on-and-off livestock grazing throughout the year, keeping habitats open, and enhancing biodiversity (Mesléard et al. 1991). Having gone from around 4000 hectares initially (Tamisier and Grillas 1994) to less than 2000 highly fragmented hectares today, they are also the most threatened habitat in the Camargue area (***Figure 1.5***). This is essentially the result of topological flattening of dune relief due to cultivation expansion.

Figure 1.5: Distribution of the Mediterranean meso-xeric grasslands (in black) in Camargue area and location of the Cassaïre site. The grey shading indicates the other wetland types in the Camargue area.

1.2.2.3. Reference choice and landscape importance in restoration

The choice of these two reference ecosystems appears logical considering their contribution to regional biodiversity. Temporary wetlands and meso-xeric grasslands are rare, adapted to Mediterranean climate, seriously endangered and enjoy a high species richness. The dry phases in temporary wetlands are often considered as a disturbance (Bonis 1998) on a par with grazing in meso-xeric grasslands (Mesléard et al. 2011). The disturbance regimes of both ecosystems should be understood so that they can be re-

established on the restored ecosystems, because they can create environmental heterogeneity and can affect community structure, diversity, and biotic interactions (Menninger et al. 2006).

Moreover, these two reference ecosystems are potentially achievable restoration targets because patches of these ecosystems remain in the Camargue area and close to the Cassaïre site (***Figure 1.4*** and ***Figure 1.5***). Indeed, reference ecosystems must be sustainable in the future (Choi et al. 2008). A landscape-scale approach can have notable implications for restoration (1) by providing better guidance for selecting reference sites and establishing project goals, and (2) by suggesting spatial configurations of restored elements appropriate for facilitating recruitment of flora and fauna, with intact regional ecosystems playing the role of propagule sources for colonizing restored areas (Cairns 1993; Bell et al. 1997; Bornette et al. 1998; Zedler 2000b; Prach et al. 2001b; del Moral et al. 2005; Moreno-Mateos and Comin 2010; Shackelford et al. 2013). The restored site can therefore have a strong influence on the relictual landscape responsible for exchanges of propagules to support a viable community, maintain biodiversity, contribute to regional dynamics, increase connectivity (Hilty et al. 2006), decrease extinction debts (Smallwood 2001; Piqueray et al. 2011), have an important role within a metacommunity context (Turnbull et al. 2000), and to potentially play the role of keystone community in fragmented landscape (Mouquet et al. 2013).

Chapter 2, ***Chapter 3***, and ***Chapter 4*** also address the importance of the landscape in plant colonization processes and community development, the distance to the nearest intact regional pool of target communities can determine whether or not species must be manually introduced to the restored site.

1.3. Ecological History of the Cassaïre site

1.3.1. Aims and methods

Ecological history is a tool that can be used to identify and characterize suitable targets for ecological restoration (Swetnam et al. 1999; Jackson and Hobbs 2009). Ecological history helps to define the state of the original ecosystem, the natural state of the landscape, and the dynamics of ecosystems. It also serves to assess the nature,

duration, and intensity of disturbances (e.g. grazing suppression, cultural eutrophication, or river containment). Even when the historical state cannot be reached, historical information for a given site can be very useful in restoration planning (Swetnam et al. 1999).

To identify the history of the Cassaïre site in the grander context of the Plan du Bourg (***Figure 1.1***), its ecological history was assessed by searching historical documentary archives, old maps, written descriptions, aerial images from 1640 to 1974 (***Table 1.1***), and by interviewing local stakeholders familiar with the period between 1946 and 2004.

Table 1.1: Documentary sources and archives for the various dates

Date	Documentary sources
1640	Provence map
1706	Rhone mouth map
1770 - 1778	Cassini map
1811 - 1829	County written description
1823 - 1828	Napoleonic land registry
1830 - 1901	Land registry
1896	Article about the sale of the Cassaïre site
1944	US Army aerial images
1947 - 1998	IGN aerial images
1946 - 2004	Interviews of the former farmer

1.3.2. Results

Today, the Plan du Bourg area is separated from the Grande Camargue by the Grand Rhône, which is one of the branches of the Rhône river (***Figure 1.1***). Conversely, a geological study demonstrated that Plan du Bourg belongs to the Camargue area (***Figure 1.6***). The 1640 map of Provence indicates that prior to the containment of the Rhône, a branch of the Rhône formerly ran along the Crau area (***Figure 1.7***) to the east of the Plan du Bourg (***Figure 1.1***). The floodwaters of the Rhône and Durance rivers formed a permanent stream, the Duransole (Colin 1904), that flowed freely through the Plan du Bourg. No written descriptions of the vegetation were found for this period, however, it is known that significant amounts of water and associated sediment inputs limited the local salinity and allowed the development non-halophilous riparian vegetation and fluvial dunes.

Cette pente n'existe que dans le Plan-du-Bourg qui n'appartient pas à la Crau, mais qui est une lisière le long du Rhône, bornée à l'Est par les étangs du Galejon, de Ligagnan, les Roubines, l'étang de Meyrane, etc. Elle fait réellement partie de la Camargue par la nature de son sol qui est limoneux et profond sans aucun galet. Autrefois elle tenait à la Camargue, parce que le Rhône coulait où coulent les Roubines qui marquent la limite de la Crau, puisque sur leur rive gauche on trouve le poudingue.

Figure 1.6: Extract from County written description, *Statistiques des Bouches-du-Rhône* (1821)

Water levels have been managed since the 14th century (de Villeneuve-Bargemon 1826) to reduce the hostility of the wetland areas and to dry out the Plan du Bourg, leading to the formation of Viguierat wetlands (currently the Viguierat National Nature Reserve) neighboring the Cassaïre site. This regional drying-out is inseparable from the Grand Rhône containment.

Figure 1.7: Provence map (Louis Cundier) indicating the former branch of the Rhône along the Crau area (1640). The Cassaïre site is located with red dot.

Maps from 1706 and 1770 indicate that the Cassaïre site once presented brush, wetlands and fluvial dunes (*Figure 1.8*), the latter having a relic distribution still present today on the site (*Figure 1.2*).

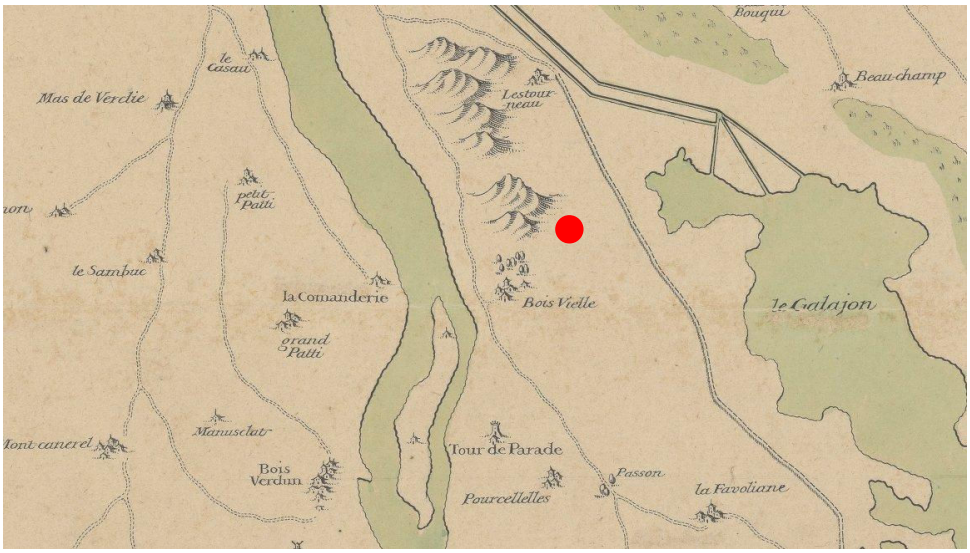


Figure 1.8: Rhône mouth map (JB Bourgignon) indicating fluvial dunes (1706). The Cassaïre site is indicated by the red dot.

The first specific indications of the Cassaïre site appear in the Napoleonic land registry (1823, *Figure 1.9*), indicating that the Cassaïre site was mainly composed of brackish marsh and flooded grassland, where grazing was common, and of small areas of vineyard and other cultivation.

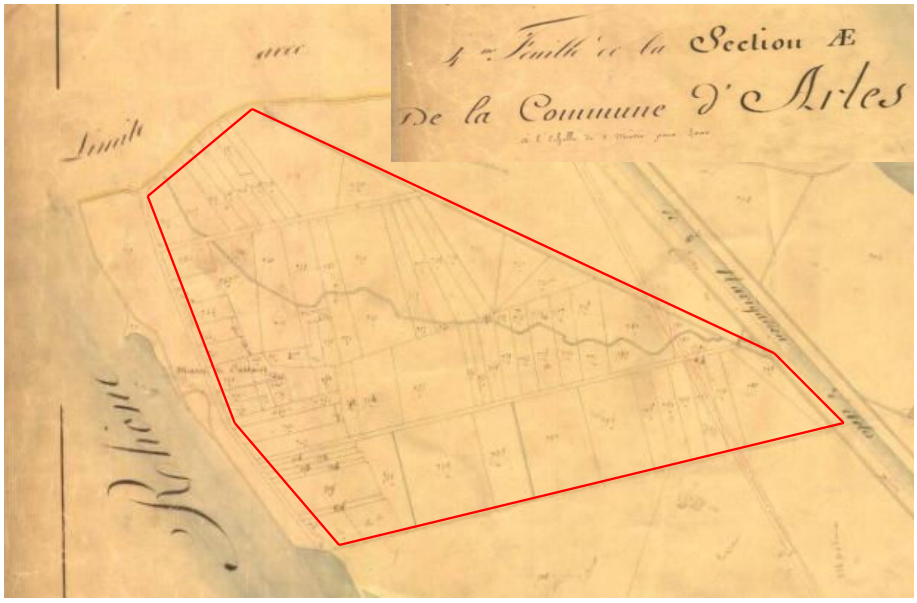


Figure 1.9: Napoleonic land registry of the Cassaïre site delimited in red (1823).

An extract from the press surrounding the sale of the site (***Figure 1.10***) indicates the presence of vineyards and other cultivation, gardens, and grassland.

Etude de Me Tardieu, avoué, à Tarascon, rue Saint-Nicolas, 25.

Vente par Licitation

Après Surenchère

à l'audience des criées tenue par le Tribunal civil de Tarascon, le vendredi dix juillet 1896, à 9 heures du matin, du

Domaine du Cassaïre

situé sur le terroir d'Arles, au Plan-du-Bourg, à vingt kilomètres d'Arles, à trois kilomètres de la gare du Mas-Thibert, ayant une halte même dans la propriété sur la ligne d'Arles à Port-Saint-Louis, d'une contenance totale de 69 hectares, 39 ares, 29 centiares ; comprenant un très beau vignoble d'une superficie de 15 hectares, jardin, terres labourables et herbages, bâtiments de maître et d'exploitation, cave avec ustensiles vinaires, greniers à foin, remises, écuries, bergerie, four à cuire le pain, forge, loge à lapins et à cochons, poulailler, habitation du jardinier. Ce domaine est longé au levant par le canal de navigation d'Arles à Port-de-Bouc et au couchant par la grande route d'Arles à Port-Saint-Louis.

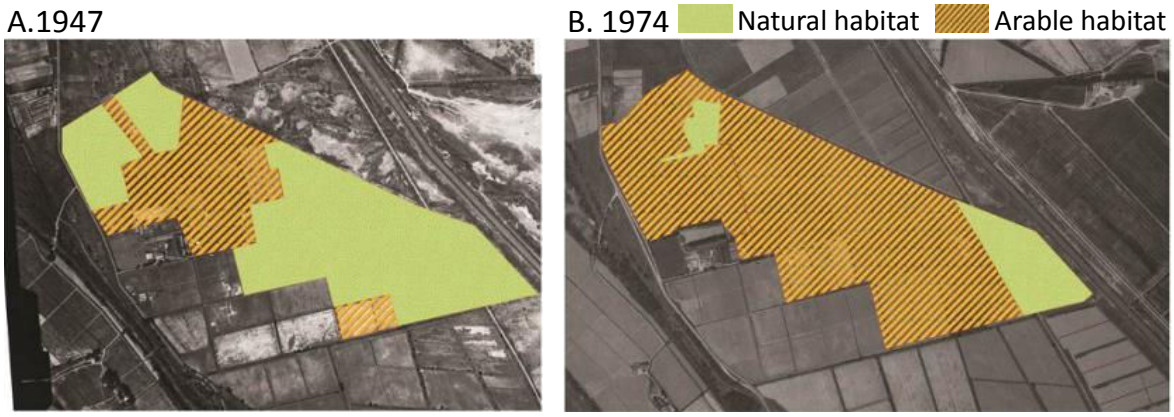
Sur la mise à prix de 23.334 fr. 16 centimes.

Pour tous renseignements, s'adresser à Arles à Me Arnaud, notaire, et à Tarascon, à Me Tardieu, avoué poursuivant.

Signé : B. TARDIEU.

Figure 1.10: Extract from the press surrounding the sale of the Cassaïre site (1896).

By digitizing and analyzing aerial images from 1947 to 1998 (e.g. ***Figure 1.11***), we detected a drastic reduction in natural habitat (from 69% to 8% of the total area, all of which corresponds to the actual relic natural habitats, ***Figure 1.2***) in favor of cultivation (from 31% to 92%, ***Figure 1.12***).



F***igure 1.11:*** Example of digitized aerial images showing the natural habitat (in green) and the arable habitat (in shaded orange) from 1947 and 1974.

The site was leveled during several decades for arable land. Wheat, sunflower, sorghum, corn, and rice (for desalinating parcels) were cultivated. Grazing was applied in autumn and winter on cultivated alfalfa or on natural grassland. In 1976, modernization of agricultural materials and practices led to a reduction in the total number of parcels, and topographic level homogenization of the remaining parcels was performed. In 2004, the site was mainly used for rice cultivation, with a few parcels reserved for wheat.

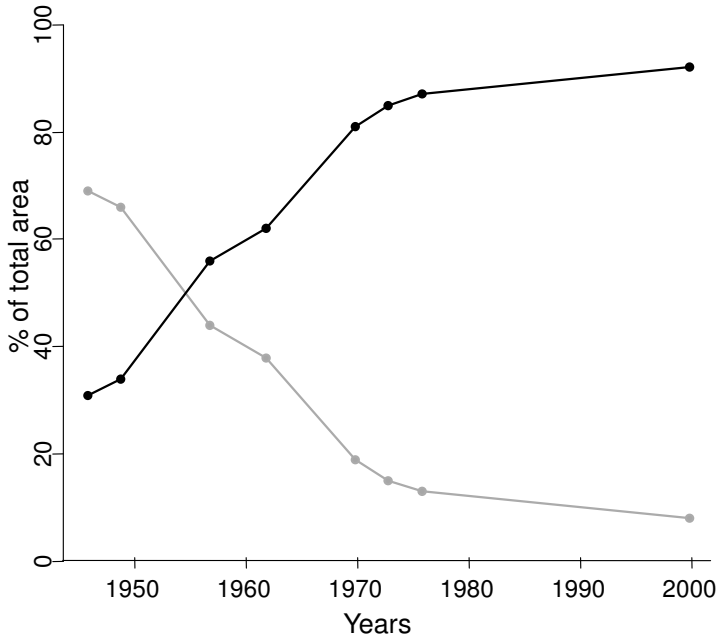


Figure 1.12: Evolution of % area in natural habitats (grey lines) and cultivated land (black lines) in the Cassaïre site between 1944 and 1998. Data collected from the analysis of digitized aerial images.

1.3.3. Confirmation of our reference ecosystems

The ecological history of the site reveals deep human imprints on ecosystems and ensures that historical restoration targets (the state prior to human impacts) cannot be reached, because they are associated with hydraulic functioning (flooding of the Rhône and Durance) that no longer exists. The specific history of the site also reinforces our choice of socio-ecosystems because it serves to ensure the actual maintenance of ecological goods and services (Choi et al. 2008; Jackson and Hobbs 2009; Davis et al. 2011). Clearly, the history of the Cassaïre area is a good illustration of the immortal words of Goethe: "Nature is ever shaping new forms: what is, has never yet been; what has been, comes not again" (Huxley 1869).

1.4. Restoration *vs.* novel ecosystem: Why restore and how do we justify restoration?

1.4.1. Restored ecosystem vs. novel ecosystem

Most ecosystems degraded by agricultural and industrial exploitation are now seen as "novel ecosystems" (Hobbs et al. 2006). Novel ecosystems are ecosystems that differ in composition and/or function from present and past systems and are a product of changing species distributions, invasive species, environmental alteration, climate change, and land use change (Harris et al. 2006; Hobbs et al. 2006). Dynamics trajectories of these novel ecosystems are multiple, and for some of them, may lead to ecosystems just as interesting as those that existed prior to human destruction (Schnitzler and Génot 2012). Some authors (Hobbs et al. 2006; Hobbs et al. 2009) have suggested that these novel ecosystems must be to the point of requiring significant attention before restoration is applied. However, a recent meta-analysis conducted over 89 ecological restoration projects concluded that restored ecosystems provide more biodiversity and ecosystem services than degraded ecosystems prior to restoration (Benayas et al. 2009).

1.4.2. Restoration on arable land

In the present context, in which the destruction of arable land continues to increase (Morel and Jean 2010) and where numerous groups fighting for access to arable land continue to emerge (e.g. *Reclaim the fields*, *Zone à Défendre* against the construction of the future airport of Notre-Dame-des-Landes, *LEOpart* against the construction of the Liaison Est-Ouest in Avignon), the opportunity and the motivation to restore natural ecosystems on arable land must be called into question. Moreover, as with all human activities, restoration must be equally subject to ethical analysis and justification (Katz 2000).

Some arguments can be given to support the restoration of Le Cassaïre site. First, the former owners had no successors and Le Conservatoire du Littoral et des Rivages Lacustres was the only potential purchaser to show any interest in acquiring the site. Unlike the high-production agricultural holdings in the Camargue area (latifundia system,

Mathevet 2004), the site of Cassaïre is a small holding with low agricultural value, and whose reliance on agricultural subsidies provided the primary basis for economic survival. Moreover, by creating a location suitable for livestock grazing, the restored ecosystem presents a new agricultural opportunity, while simultaneously offering new services, such as hunting. Finally, although it would be ethically, financially, and ecologically undesirable to do so, the entire restoration operation could be completely reversed if arable land was needed later, and this is something that cannot be said for former agricultural land that has been filled in with concrete.

Transition to Chapter 2

After defining the main objective of the project restoration of the Cassaïre in ***Chapter 1*** (i.e. the reference ecosystems), ***Chapter 2*** examines the plant community dynamics after the restoration of abiotic conditions.

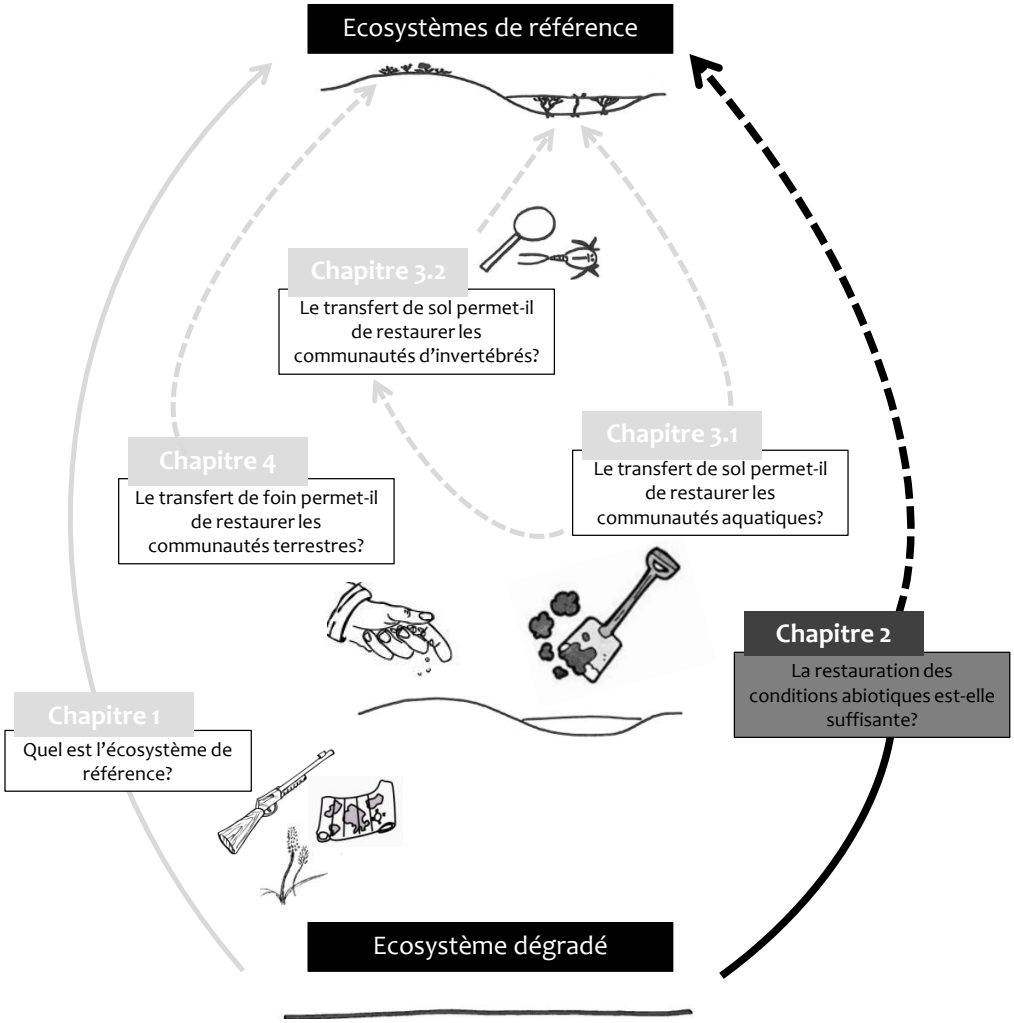


Figure T2.1: Location of ***Chapter 2*** in the general thesis organization

The study of the initial state (*To*; Willm et al. 2011) is a crucial to evaluate the potential of the degraded ecosystem. This study revealed a low species richness and a relatively homogeneous species composition on former agricultural fields, with the dominance of two meadow species *Lolium perenne* L. and *Trifolium repens* L.. No ecological values can be expected for this ecosystem even in the long term as the practices of rice cultivation led to a totally homogenization of the topography and the improvement of abiotic conditions is require to try to achieve our 2 reference communities, dealt in ***Chapter 2***.

Seed rain trap with windsock at 1.90 m high.
In foreground an experimental block filled with water.

Soil cores to analyze the Cassaïre soil seed bank.

Chapter 2 - Regional pool species: relative contribution of seed bank, seed rain, and extant vegetation in aquatic and terrestrial ecosystem

Isabelle Muller, François Mesléard, Julie Chenot & Elise Buisson

2.1. Introduction

Ecological restoration and ecological creation, as implemented on areas of former arable land, are used to promote a more diverse plant community, and they have recently become a part of general conservation practice (Millennium Ecosystem Assessment 2005). Creation (restoration *sensu lato*) is the establishment of a community on a site where all traces of its previous existence have been largely, or totally, removed (Anderson 1995). It differs from restoration *sensu stricto* which consists of managing existing resources to return the habitat to a desirable state (Society for Ecological Restoration 2004). In both cases, the objective is to establish a reference community that complies with conservation targets (e.g. target vegetation, target species, etc.). Although many restoration scientists equate restoration with accelerating succession towards the reference community (Zedler 2000a), the use of natural revegetation processes for restoration, a process known as the spontaneous succession approach or the passive restoration approach, has not been sufficiently explored. Such methods should always be carried out before resorting to labor-intensive operations (Mitsch and Wilson 1996; Zedler 2000a; Prach et al. 2001b; Prach and Hobbs 2008). Bradshaw (1996) recommends using the spontaneous succession approach wherever possible, because it is relatively inexpensive, saves time and effort, can be used on a large scale, and is likely to be self sustaining, generally because processes involved originate from nature. Investigating natural revegetation and colonization processes is therefore important because it can provide necessary information for restoration ecology (Bobbink and Willems 1993; Prach et al. 2001b; Prach and Hobbs 2008; Török et al. 2009). Indeed, determining seed availability and characteristics (i.e. target, unwanted, or alien) should help to predict future plant composition, allowing restoration practitioners to make educated decisions and implement appropriate measures.

Plant community succession is driven by many factors, but ultimately, the regional species pool is the primary determinant of community composition (Keddy 1992; Strykstra et al. 1998; Zobel et al. 1998; Lortie et al. 2004). The regional species pool has two origins: external, and internal to the community in question. The external species pool is composed of species found in the landscape surrounding the site that must be brought into the site. It is therefore dependent on species' dispersal capacities and on

their distance to the site. The internal species pool is composed of species already present on site, in the soil seed bank, or in the extant vegetation (Fattorini and Halle 2004). Evaluating the potential for spontaneous succession requires the determination of the availability of propagules dispersed to the site (i.e. seed rain), of propagules stored in the soil (i.e. soil seed bank), and of propagules coming from extant vegetation (Strykstra et al. 1998; Zobel et al. 1998). More than identifying the future plant composition and the potential limitations of restoration success, evaluating the potential of spontaneous succession provides an ideal experimental setting i) to test the theory of community assembly (i.e. acid test, Bradshaw 1996), and ii) to identify the contribution of each pool (i.e. soil seed bank and seed rain) to regeneration and, by extension, to the plant community.

Seed banks provide information on past vegetation, land-use history (Adams and Steigerwalt 2011; Török et al. 2011a), and regeneration potential (Hopfensperger 2007). Seed rain is generated via two distinct mechanisms: short-distance dispersal, corresponding to the auto-regeneration capacity of the extant vegetation through local seed production, and long-distance dispersal, which is typically rare but crucial to population spread (Soons et al. 2004; Soons and Ozinga 2005; Trakhtenbrot et al. 2005; Nathan 2006) and to plant community modification. In practice, most dispersing events occur relatively at short distances away from the source (Trakhtenbrot et al. 2005). Seed rain characterization often requires intense work, as it relies on a large network of traps with different configurations in order to be able to characterize the different dispersal processes (Greene and Johnson 1996; Chabrerie and Alard 2005).

Grassland and wetland ecosystem restoration commonly aims at both introducing target species and recovering ecosystem functions. The main difference between these two types of ecosystem is that unlike grasslands, wetlands exhibit structure and functioning that is strongly regulated by hydrological conditions (Grillas 1990; Zedler 2000b). The highly specific conditions of periodic flooding often make the trajectories of wetland ecosystems very predictable (Mesléard et al. 1991) when compared to more open and fluctuating systems such as grassland. Moreover, in wetland ecosystems, some propagules are small in size compared to terrestrial ones and are therefore more easily dispersed (Bradshaw 1996). Several studies have shown that long distance dispersals are

rare events in terrestrial situations (Harper 1977; Willson 1993) and are probably more prevalent in wetland systems (Kinlan and Gaines 2003; Kinlan et al. 2005).

Contrasting results have been reported with the spontaneous succession approach. In terrestrial situations, even though some studies have shown a high degree of re-establishment from the regional species pool in grassland restoration (Gibson and Brown 1992; Etienne et al. 1998; Matus et al. 2003), numerous other studies have found a relatively low potential to recover through a long-term seed bank or through long-distance seed rain (Graham and Hutchings 1988; Bakker et al. 1996; Hutchings and Booth 1996; Kalamees and Zobel 2002; Donath et al. 2003; Buisson et al. 2006a). Identically contrasting results have been reported in aquatic situations, with some studies showing successful passive restoration (Valk et al. 1992; Galatowitsch and Valk 1996; Elmarsdottir et al. 2003; Leck 2003; Combroux and Bornette 2004; De Steven et al. 2006) and others not, while indicating a lack of native species in the seed bank and seed rain (Kettenring and Galatowitsch 2011; Beas et al. 2013).

The limitations of plant recolonization through spontaneous succession can be explained by: (1) the fragmented landscape context, which is not favorable to species dispersion, and which impacts the seed rain (Ash et al. 1994); (2) the effect of the agricultural disturbance, which often may involve fertilization and ploughing, each of which can have a lasting and direct impact on the soil seed bank and plant community (Gibson and Brown 1992; Clements et al. 1996); (3) the influence of stronger recolonizers coming from a disturbed landscape or from disturbed plant communities: these can prevent the establishment of native plant communities in terrestrial (Prach et al. 2001b) and aquatic systems (Kettenring and Galatowitsch 2011); and (4) the ability of target species that have short-lived seeds (Römermann et al. 2005; Buisson et al. 2006a; Rowarth et al. 2007) or limited dispersal abilities (Buisson et al. 2006a; Kettenring and Galatowitsch 2011) to disperse and to establish a persistent seed bank.

In addition to availability of seeds, which either originate from seed rain or from soil seed bank, site limitation, corresponding to inappropriate site conditions, may also hamper the re-establishment of vegetation. Indeed, plant community assembly depends strongly on abiotic processes (Galatowitsch and Valk 1996; Lepš 1999; Bischoff 2002; Hobbs and Norton 2004; Kiehl et al. 2010; Bornette and Puijalon 2011), and the long term

success of a restoration project depends on the suitability of the abiotic conditions. If such conditions are drastically altered and are adverse to the target vegetation, their restoration will have to precede spontaneous succession (Prach et al. 2001b).

In the Mediterranean basin, temporary wetlands and meso-xeric grasslands are two of the priority habitats listed by the Natura 2000 Network of the European Union Habitats directive (European Commission 1992). They both have been greatly impacted by agriculture expansion. Rice cultivation has been especially onerous because of its leveling requirement and its need for fertilization, which have respectively eliminated variations in topography and trophic levels. In Mediterranean temporary wetlands, the hydrological regime appears to be one of the main factors controlling the plant community (Grillas 1990), whereas the nutrient level appears to strongly affect oligotrophic grassland communities adapted to nutrient-poor soils (Lepš 1999; Kiehl et al. 2010). To restore favorable abiotic conditions for these two ecosystems in former ricefields, topsoil can be removed, leading to i) the creation of depressions, which allows the restoration of wetland hydrological conditions, ii) a reduction of nutrient levels, favoring the development species adapted to low-nutrient conditions (Marrs 2002), and iii) the removal of the topsoil seed bank, which is often dominated by ruderal species (Davy 2008; Török et al. 2011a).

This chapter aims to assess the regional species pool and the potential for spontaneous succession in terrestrial and aquatic communities on former ricefields after topsoil removal (corresponding to the abiotic conditions restoration). In other words, we make an attempt at answering the following general question: can the restoration of abiotic conditions (assuming that abiotic condition are restored with topsoil removal for grassland and topsoil removal and hydrological regime for wetland) in terrestrial and aquatic communities be sufficient to establish target species, and are the two communities different from a restoration standpoint? To address this question, we studied experimentally the species present in the seed bank, seed rain, and extant vegetation at 4 different topsoil removal depths. The results of these studies were used to plan management strategies appropriate for creating temporary wetlands and meso-xeric grasslands in the aftermath of rice cultivation. Seed banks were studied in terrestrial and aquatic conditions to test the potentiality for terrestrial and aquatic ecosystem

restoration. Seed rain was evaluated using three methods, one characterizing long distance dispersion, another characterizing the auto-regeneration capacity of vegetation through local seed production, and a final method characterizing hydrochory transport. By restoring (or at least by improving) abiotic conditions, and allowing spontaneous succession to occur, we were able to investigate the following four questions: (1) What can be expected from the soil seed bank, the seed rain, and extant vegetation i.e. the proportion of alien and target species in the regional species pool. We hypothesized a low number of species and of individuals of target species in the regional species pool after ricefield disturbance; (2) What are the impacts of abiotic conditions restoration on soil seed bank and seed rain i.e. determine the composition of soil seed bank and seed rain at different depths. We hypothesized that the seed rain continues to supply new recruitments at all depths (i.e. same contribution of seed rain at all depths) while there would be a decrease in density of seeds and in species richness in the seed bank with depth in terrestrial and aquatic conditions; (3) To what extent soil seed bank and seed rain influence the extant vegetation i.e. determine the similarity between extant vegetation, soil seed bank and seed rain between the different depths. We hypothesized that with increasing topsoil removal depth, the influence of the soil seed bank decreases and thus the influence of the seed rain proportionally increases; and (4) Is there difference between temporary wetland and meso-xeric grassland ecosystem restoration on former ricefields? We hypothesized that it is easier to restore abiotic conditions for wetland ecosystem (abiotic filters are easier to control in wetland ecosystem than in grassland ecosystem), that seed dispersal is less limited in wetland ecosystem (because seeds are generally smaller and because hydrochory play an additional role) therefore making them easier to restore using spontaneous succession.

2.2. Materials and Methods

2.2.1. Study site

The experiment was conducted at the Cassaïre site (c. 43°31’ N, 4°44’ E, 3 m maximum elevation) located east of the Camargue area (Rhône delta, Southern France). The climate is typically Mediterranean, characterized by an annual average temperature of 15°C, an

annual rainfall of 550 mm mainly concentrated in autumn, and a summer drought (Heurteaux 1970).

For period of more than 60 years, the study site, which is composed of four principal parcels (***Figure 2.1.A***), has been mainly subjected to rice cultivation, which definitively ended in 2004.

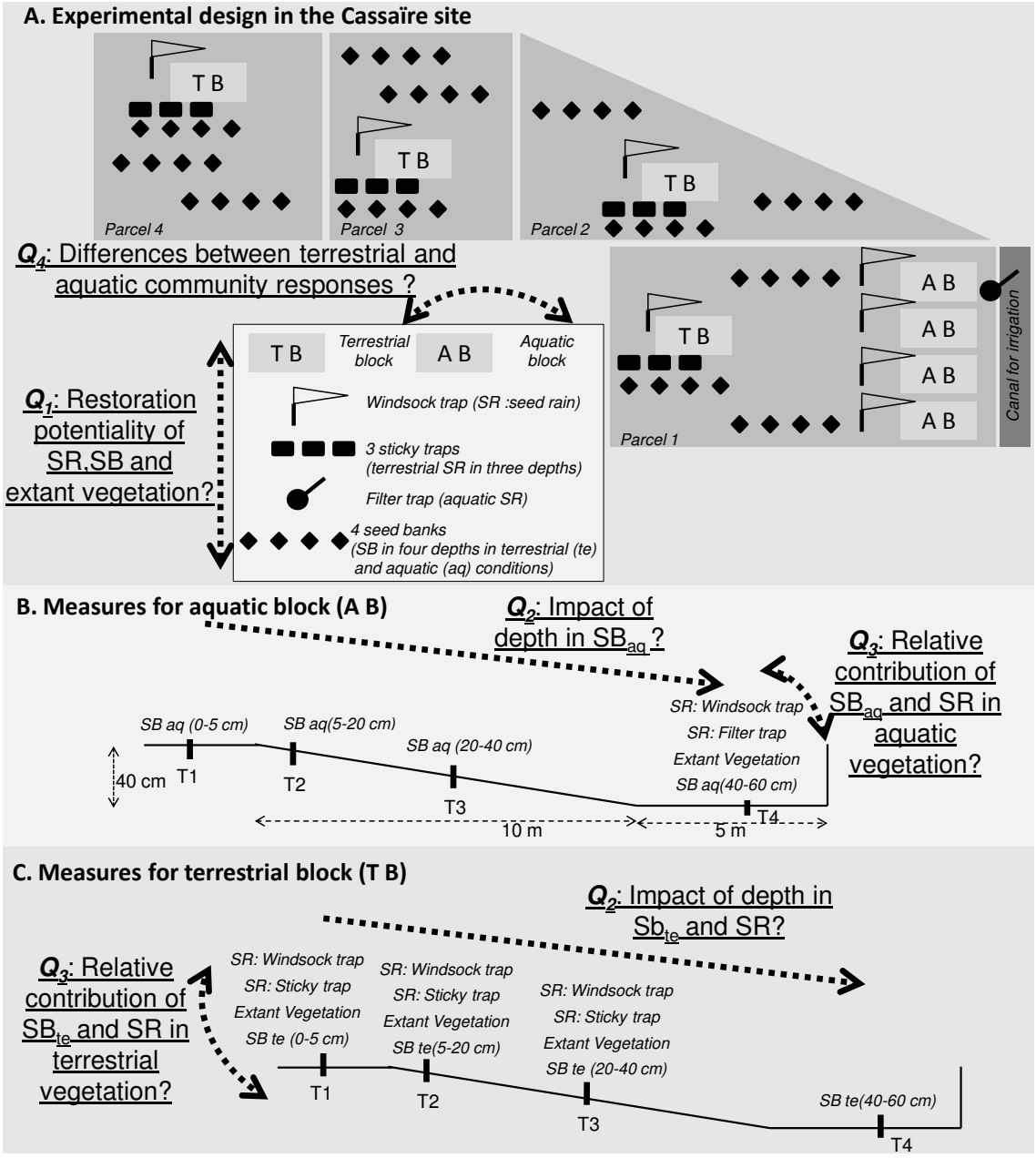


Figure 2.1: Sampling design of seed bank, seed rain, and extant vegetation for terrestrial and aquatic blocks and illustration of the different study questions.

The technical agricultural itinerary of rice cultivation includes plowing to a 20 cm depth in winter, soil leveling and fertilization before impoundment and planting in April,

and finally harvesting in September (Marnotte et al. 2006). Recurrent leveling led to the complete elimination of the natural topography.

Mediterranean temporary wetlands are characterized by winter and spring flooding, the durations of which vary greatly from year to year, and by a complete drying-out in the summer (Grillas et al. 2004). Plant communities in these wetlands are mainly driven by the hydroperiod, water depth, and salinity (Grillas 1990). Mediterranean meso-xeric grasslands are characterized by a high proportion of annuals (Molinier and Tallon 1970; Braun-Blanquet 1973), are managed by traditional extensive on-and-off livestock grazing (Mesléard et al. 2011), and are associated with nutrient-poor soils.

2.2.2. Abiotic conditions for restoration

Eight mesocosms, henceforth referred to as blocks, were dug out with a gentle slope (15 m long × 5 m wide × 40 cm deep; ***Figure 2.1.B***). Four blocks were randomly selected (one on each parcel; ***Figure 2.1.A***) for use in terrestrial vegetation monitoring (***Figure 2.1.B***). The four remaining blocks were set up along an irrigation canal and used for aquatic vegetation monitoring (***Figure 2.1.B***). A pump maintained a constant 20 cm water level in those four blocks from January 2012 (four months after classical temporary wetland conditions but allowing even so the germination of vernal species germination in March) to the end of May 2012, simulating hydrological conditions of temporary wetlands. To mimic the effects of grazing that reference grasslands are typically subject to, we mowed and exported the cuttings around the terrestrial blocks in January 2012.

2.2.3. Vegetation monitoring

Vegetation monitoring in the four terrestrial blocks was carried out along three permanent transects on each block (***Figure 2.1.B*** and ***Figure 2.1.C***): one at the top of the block (transect 1 (T1), corresponding to the vegetation without topsoil removal), one at 1 m from the top of the slope (transect 2 (T2), corresponding to 5 cm of topsoil removal), and one at 6 m from the top, or the middle of the slope (transect 3 (T3), corresponding to 20 cm of topsoil removal).

The vegetation survey was carried out using one 30 × 30 cm permanent plot subdivided into nine 10 × 10 cm cells. The plot was positioned at the middle of each transect, corresponding to the middle of the block. In May 2012, the presence/absence of all species was recorded in each cell, obtaining abundance data for each species.

In aquatic blocks, vegetation monitoring was carried out only along one transect at 12.5 m from the top of the block, which is the bottom of the block (transect 4 (T4), corresponding to 40 cm of topsoil removal; (***Figure 2.1.B*** and ***Figure 2.1.C***)), using a 4 × 2 m plot. In each plot, we estimated the % cover of each species. Plots were monitored in May 2012.

2.2.4. Soil seed bank

In order to determine the influence of topsoil removal on the soil seed bank and the potential role of buried seeds in the succession, we collected 12 soil samples (three on each parcel, randomly selected; ***Figure 2.1.A***) i) from the surface (0 to 5 cm deep, corresponding to the first transect), ii) from 5 to 20 cm deep (corresponding to the second transect), iii) from 20 to 40 cm deep (corresponding to the third transect) and iv) from 40 to 60 deep (corresponding to transect 4). For each sample composed of 3 pooled sub-samples, 1 L total of soil was taken in January 2011. The soil seed bank was evaluated using the method of seedling emergence with sample concentration (Ter Heerdt et al. 1996). Each sample was cleaned with water and passed through a 200-micron sieve in order to separate the seeds from the clay before spreading them on 30 x 20 cm trays filled with a 50%/50% mix of organic matter and vermiculite, coated 100-micron medical gauze, which was intended to prevent the seeds from sinking into the substrate. In order to have both terrestrial and aquatic seed bank species, we used two germination conditions. First, terrestrial conditions were applied: trays were watered regularly to provide moist soil during the ten-month germination period. Germinated seedlings were identified, counted, and removed every week to avoid potential competition. Unidentifiable plants were transferred to pots and allowed to grow so that their identities could be established later. After this, samples were stored at 4°C for two months, before the aquatic conditions were applied. Trays were then placed in a submerged setting (in 10 cm of standing water) for six months. Germinated seedlings

were identified as explained previously. For both the aquatic and terrestrial studies, trays filled with the same substrate and coated with medical gauze were set up as controls, principally to rule out the possibility of spontaneous germination from the organic matter or from accidental seed rain in the greenhouse.

2.2.5. Seed rain

In order to provide a reliable estimate of the seed rain, we used three types of seed traps, each optimized for a different seed dispersal process (Chabrerie and Alard 2005). On each block, one windsock trap was placed for 7 months (from July to September 2011 and from March to July 2012, to cover the main seed production season, ***Figure 2.1.A***). On each terrestrial block, three sticky traps were placed close to the ground during same 7-month period (***Figure 2.1.A***). For the four aquatic blocks we addressed a single filter trap, placed during the inundation period from January to May 2012 (***Figure 2.1.A***). All seed traps were associated with a vegetation sample and a soil seed bank sample in order to assess their similarity.

The sticky traps were constructed from 20 x 30 cm pieces of clear Plexiglas plate coated with clear sticky grease and held in place on the ground with metal poles (our traps are similar to those used in Rand 2000; Chabrerie and Alard 2005; Kettenring and Galatowitsch 2011). The sticky traps were placed on transects 1 (to sample seed rain at the surface), 2 (at 5 cm of topsoil removal), and 3 (at 20 cm of topsoil removal), close to the sample vegetation in each block (three seed rain samples per terrestrial block) (***Figure 2.1.A***). Because of the potential for inundation by rainfall, no sticky traps were placed on transect 4 on the terrestrial block, and none were placed to the aquatic blocks (where filter traps were used instead). The characteristics of the sticky traps were chosen to record the auto-regeneration capacity of extant vegetation through local seed production. Over the sample period, exposed sticky traps were swapped out for fresh ones on a monthly basis. Seeds were extracted from sticky traps by scraping the seeds from the traps. Then the seeds were identified under a binocular microscope by comparison with a reference collection of the extant vegetation seeds from the study site.

The windsock trap consisted of a 25 cm diameter, 1.20 m long windsock affixed to a 1.5 m high wooden post. Seeds were collected in a 100 µm-mesh filter gauze bag stapled to the base of each windsock. One windsock trap was placed at the top of each block, close to the vegetation sample and the sticky trap of transect 1, with the assumption that the seed rain should be identical for all transects. Indeed, the characteristics of the windsock trap were chosen to record principally anemochorous species and long-dispersal events. The bags were replaced every month from July to September 2011 and from March to July 2012, and the seeds were identified in the same way as for sticky traps.

The filter trap consisted of filtering the water from the irrigation channel used to fill the aquatic blocks. Once a month, during the inundation period from January to May 2012, we filtered the water for 30 minutes through a 100-µm mesh, and repeated this process three times. The characteristics of the filter trap were chosen to collect hydrochorous species, and seeds from this trap were identified in the same way as for the other two traps.

Because the sampling area was not the same for the windsocks and the sticky traps, we divided the number of collected seeds per the surface area sampled (600 cm^2 for the sticky trap and 491 cm^2 for the windsock trap), to facilitate data comparison between the two types of trap. Monthly samples from each trap were summed to obtain an effective annual seed rain.

2.2.6. Data analysis

Question 1 (restoration potential) and question 4 (differences between terrestrial and aquatic community responses) are qualitative, and therefore answerable without using any statistical analyses.

Question 2 (Impact of depth), for which we studied the effect of abiotic conditions on soil seed bank and seed rain, led to a comparison of species richness and density among the different depths. This was done using ANOVA when parametric assumptions were justified, and using Kruskal-Wallis, when data were not normally distributed, followed by Tukey tests (Sokal and Rohlf 1995) or pairwise Wilcoxon comparisons with a *p*-value adjustment according to Holm's method (Holm 1979). We compared species richness and densities of the seed bank between the two germination conditions with

Student-t tests, when parametric assumptions were valid, or with Wilcoxon tests, when data were not normally distributed. We also ran a Correspondence Analysis (CA; Greenacre 1984), based on seed density per cm^2, for species collected in the windsock and sticky traps.

Question 3 (relative contribution of seed bank and seed rain in vegetation), for which we measure similarity between the extant vegetation, soil seed bank, and seed rain, we associated a seed bank and a seed rain sample with each extant vegetation sample. For aquatic blocks, only the soil seed bank from parcel 4 was used in our similarity evaluation. We ran one Correspondence Analysis based on the presence/absence of species on terrestrial extant vegetation (terrestrial blocks), terrestrial soil seed bank, and terrestrial seed rain (sticky traps + windsock traps). We also ran a similar CA on the aquatic extant vegetation (aquatic blocks), the aquatic soil seed bank, and the aquatic seed rain (filter traps + windsock traps). For each pool (seed bank, seed rain, and extant vegetation), species abundances were converted to species frequencies (species frequency = the number of seeds of a given species, or the number of abundances of a given species / the total number of seeds in the compartment, or the total number of abundances × 100). For terrestrial blocks at all three depths, the correlation in species frequency between seed bank and extant vegetation and between seed rain and extant vegetation were analyzed using Spearman rank correlation coefficients. For aquatic blocks, the correlations were analyzed using Pearson correlation coefficient. The Sorensen similarity index was used to measure the species similarity between seed bank and extant vegetation, between seed rain and extant vegetation, between seed rain and seed bank in aquatic blocks, and among the three depths in terrestrial blocks. The comparisons among the Sorensen indices were made using ANOVA for those cases where parametric assumptions were justified, and Kruskal-Wallis, when the data were not normally distributed.

2.3. Results

2.3.1. Restoration potential from the regional species pool

In total, 64 species were recorded in the regional species pool (extant vegetation, seed bank, and seed rain, ***Table 2.1)***.

Table 2.1: Species present in seed bank, seed rain, and extant vegetation in terrestrial and aquatic conditions. Target species are in bold type in the table.

	Terrestrial condition			*Aquatic condition*		
	Seed bank	Extant vegetation	seed rain	Seed bank	Extant vegetation	seed rain
Amaranthus sp			×			
Ammannia coccinea	×					
Lysimachia arvensis	×	×	×			
Arundi donax			×			
Aster squamatus	×	×	×			
Avena barbata		×	×			
Bolboschoenus maritimus				×	×	
Brachypodium distachyon			×			
Bromus hordeaceus		×	×			
Bromus madritensis		×	×			
Bromus rubens			×			
Bromus sterilis		×	×			
Carex divisa	×		×			
Carex sp					×	×
Centaurium spicatum	×					
Chara braunii				×		
Chara vulgaris				×	×	×
Chenopodium album		×	×			
Chladophora vagabunda					×	
Cirsium arvense			×			×
Conyza sumatrensis	×		×			
Cyperus difformis	×			×		
Cyperus eragrostis	×					
Cyperus fuscus	×					
Daucus carota	×					
Echinochloa sp	×					
Epilobium tetragonum	×					
Erigeron canadense	×					
Heteranthera reniformis						×
Holcus lanatus	×	×	×			×
Hordeum marinum		×	×			
Hordeum murinum		×	×			
Juncus articulatus	×			×	×	
Joncus bufonius	×		×			
Lactuca saligna		×				
Lactuca seriola		×	×			×
Lamiaceae sp			×			×
Lindernia dubia	×			×	×	
Lolium perenne		×				
Lolium rigidum		×	×			×
Lotus tenuis	×	×	×			
Lycopus europaeus						×
Lythrum hyssopifolia	×					
Medicago lupulina	×	×	×			
Medicago polymorpha	×					
Melilotus indicus	×					
Paspalum distichum	×	×				
Phragmites australis					×	
Picris echioïdes	×	×	×			×
Picris hieracioides		×	×			
Picris pauciflora			×			
Plantago coronopus	×	×				
Plantago lanceolata	×	×				×
Plantago major	×	×	×			
Poa annua		×	×			
Poa trivialis	×	×	×		×	×
Polygonum aviculare	×	×	×			
Polygonum lapathifolium			×			
Polypogon bellardii	×	×	×			
Polygonum persicaria	×		×			
Populus alba					×	
Pulicaria dysenterica	×					
Rumex crispus	×	×	×		×	
Salix fragilis	×					
Samolus valerandi	×					
Schoenoplectus mucronatus						×
Schoenoplectus supinus	×			×		
Sonchus arvensis			×			
Sonchus asper			×			
Sonchus oleraceus	×		×		×	×
Tamarix sp	×					
Trifolium campestre	×					
Trifolium repens	×	×	×			
Typha laxmanii	×				×	

Only nine target species of meso-xeric grasslands were recorded, five in the seed rain (both in windsock and sticky traps; *Brachypodium distachyon* (L.), P.Beauv., *Bromus hordeaceus* L., *Bromus madritensis* L., *Carex divisa* Huds. and *Hordeum marinum* Huds.), and five in the terrestrial soil seed bank (at the 4 depths; *Carex divisa* Huds., *Centaurium spicatum* (L.) Fritsch ex Janch., *Medicago polymorpha* L., *Plantago coronopus* L. and *Trifolium campestre* Schreb.), although each of these exhibited a low frequency (less than 3%).

Four of these target species were also recorded in the extant vegetation (three were also present in the seed rain: *Bromus hordeaceus* L., *Bromus madritensis* L. and *Hordeum marinum* Huds., and one was present in the seed bank: *Plantago coronopus* L.). No temporary wetlands target species were found in the seed rain as captured by the filter traps or in the aquatic soil seed bank. In contrast, several of the exotic species were found in the seed bank and in the seed rain (in both terrestrial and aquatic conditions), considered as invasive for France (Conservatoire Botanique National Méditerranée 2012), such as *Arundo donax* L. or *Symphyotrichum subulatum* var. *squamatum* (Spreng.) S.D.Sundb., or exotic ricefield weeds, such as *Heterenthera reniformis* Ruiz & Pav., *Ammannia × coccinea* Rottb. or *Lindernia dubia* (L.) Pennell (Marnotte et al. 2006; Mouronval and Baudouin 2010).

2.3.2. Soil seed bank

In total, 7159 individuals germinated from the soil seed bank representing a total of 49 species. The terrestrial seedling emergence experiment allowed us to identify a total of 5639 seedlings representing 41 species, and the aquatic experiment resulted in a total of 1520 seedlings, representing 17 identified species, with 8 species exclusive to the aquatic condition, mainly belonging to the charophyte division. The number of seedlings (***Figure 2.2.A***) and of species richness (***Figure 2.2.B***) in the soil seed bank was significantly higher in the terrestrial conditions (117.5±13.4 for number of seedlings; 13.1±0.6 for species richness) than in the aquatic ones (31.7±4.7 for number of seedlings; 3.5±0.3 for species richness).

Soil seed bank density and species richness changed with depth in both aquatic and terrestrial conditions (***Figure 2.3***). The number of seedlings in the soil seed bank declined

significantly when going from 0-5 cm deep to 5-20 cm deep in the terrestrial condition (***Figure 2.3.I.A***) and in the aquatic condition (***Figure 2.3.II.A***). However, no difference was observed between the 5-20 cm, 20-40 cm, and the 40-60 cm depths in the terrestrial (***Figure 2.3.I.A***) and aquatic conditions (***Figure 2.3.II.A***). The species richness was also observed to decline between the 0-5 cm and the 5-20 cm depths in the terrestrial condition, no difference was found between the two deeper ranges, and a second significant decrease was found between the 20-40 cm and the 40-60 cm depths (***Figure 2.3.I.B***). In the aquatic condition a significant decrease in species richness was only observed between the 0-5 cm and the 40-60 cm depths (***Figure 2.3.II.B***).

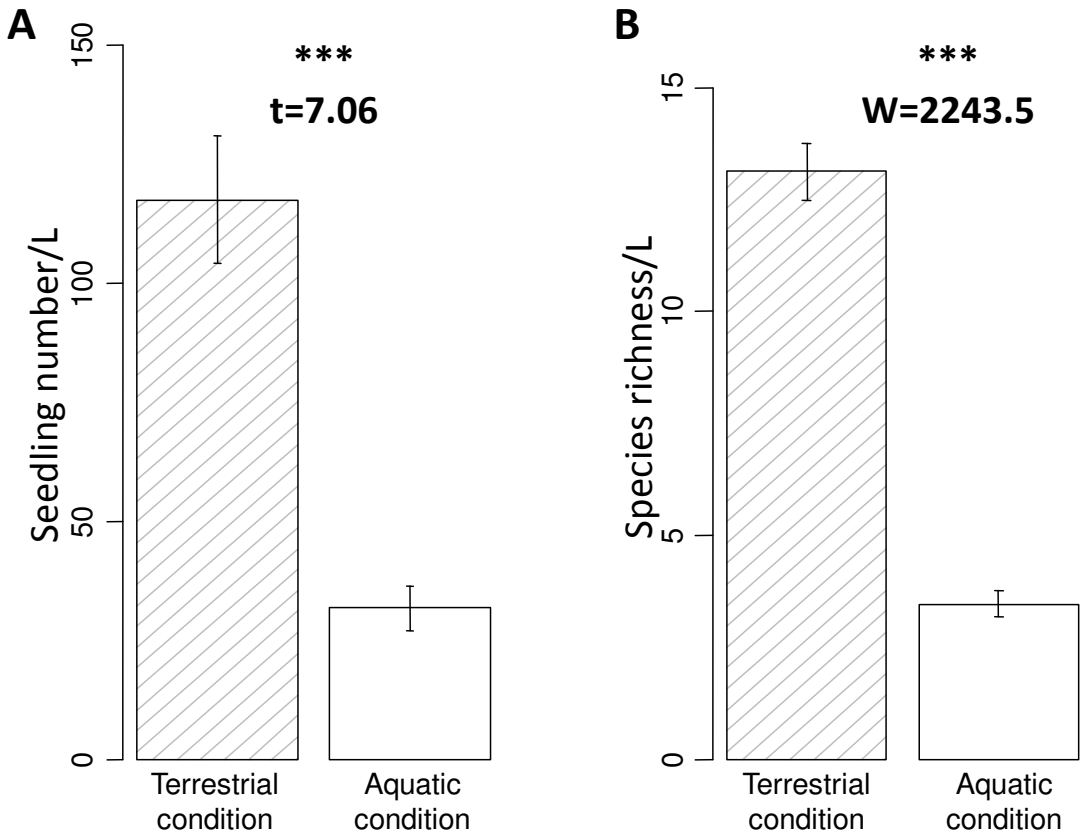


Figure 2.2: Mean and standard errors of A) seedling number in soil seed bank per liter and B) species richness in soil seed bank per liter of the Cassaïre site in terrestrial (shaded bars, n=48 plots) and aquatic (white bars, n=48 plots) conditions. The t of Student and the *W* of Wilcoxon tests performed are shown above the bars (***: p<0.001).

The dominant species in the soil seed bank were the same for each depth in terrestrial and in aquatic conditions. The dominant species in terrestrial condition across all depths was *Juncus bufonius* L. (contributing up to 27 % of the total number of

seedlings), an amphibian annual species present on wet sandy substrates in the Camargue area but favored by rice cultivation (Marnotte et al. 2006). Next in importance were *Ammannia × coccinea* Rottb. (contributing up to 12% of the total seedling number), *Lindernia dubia* (L.) Pennell (contributing up to 8% of the total seedling number), and *Cyperus difformis* L. (contributing up to 9% of the total seedling number), all of which are typical exotic ricefield weeds (Marnotte et al. 2006). Last of all was *Trifolium repens* L. (contributing to 10% to the total seedling number), a mesophyllous meadow species.

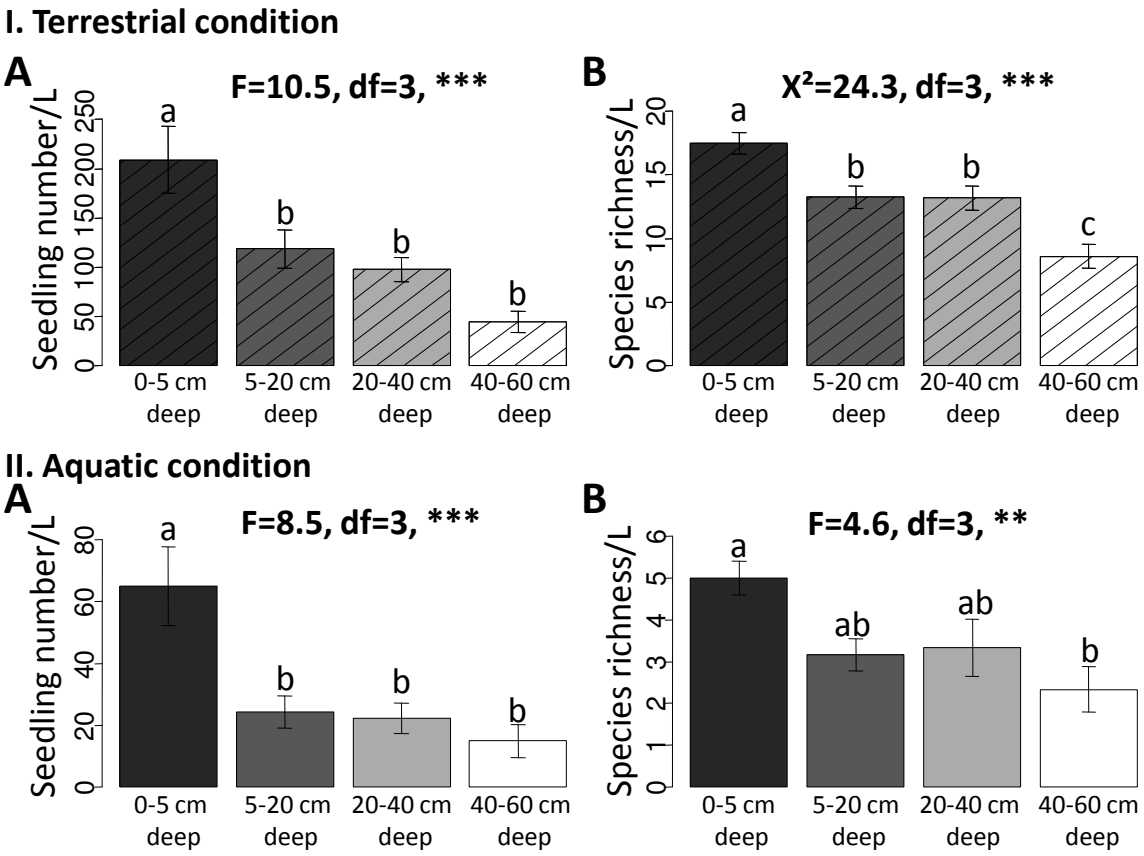


Figure 2.3: Mean and standard errors of A) seedling number per soil liter in the soil seed bank, B) species richness per soil liter in the soil seed bank at the Cassaïre site in (I) terrestrial conditions, at 0 to 5 cm deep (shaded black bars, n = 12 plots), 5 to 20 cm deep (shaded dark grey bars, n = 12 plots), 20 to 40 cm deep (shaded light grey bars, n = 12 plots) and in 40 to 60 cm deep (shaded white bars, n=12 plots) and in (II) aquatic conditions, at 0 to 5 cm deep (black bars, n = 12 plots), 5 to 20 cm deep (dark grey bars, n = 12 plots), 20 to 40 cm deep (light grey bars, n = 12 plots), and 40 to 60 cm deep (white bars, n=12 plots). The F of ANOVA or the χ^2 of Kruskal–Wallis tests performed are shown above the bars (**: p<0.01; ***: p < 0.001), bars showing the same letters do not have any significant differences according to Tukey tests or to pairwise Wilcoxon multiple comparisons with Holm p adjustment.

In aquatic conditions, the most dominant species across depths were *Juncus articulatus* var. *articulates* (contributing up to 29 % of the total seedling number), *Schoenoplectus supinus* (L.) Palla (contributing up to 28 % of the total seedling number); these are two other exotics typical ricefield weeds (Marnotte et al. 2006), *Lindernia dubia* (L.) Pennell (contributing up to 12% of the total seedling number), *Cyperus difformis* L. (contributing up to 10% of the total seedling number), and *Chara vulgaris* L. (contributing up to 7% of the total seedling number), a banal algae enhanced by rice water management (Mouronval and Baudouin 2010).

2.3.3. Seed rain

Forty-four species among the 3259 seeds collected were identified in the seed rain (by windsock, sticky, and filter traps). We recorded 10.3±3.7 species per sticky trap on average (in total, 31 species were recorded by sticky trap), 10.0±1.2 species per windsock trap (in total 23 species were recorded by windsock) and only 0.86±0.2 species per filter trap. Only five species were recorded in total in the filter traps (*Carex sp., Chara vulgaris* L., *Heterenthera reniformis* Ruiz & Pav., *Lycopus europaeus* L. and *Schoenoplectus mucronatus* (L.) Palla).

Differences in composition were observed between the two terrestrial traps (***Figure 2.4***): the first axis of the CA (18.2%) discriminated the sticky traps capturing *Polygonum aviculare* L., *Polygonum bellardii* All., *Holcus lanatus* L., and *Lolium rigidum* Gaudin from the windsock traps capturing *Picris pauciflora* Willd, *Cirsium arvense* (L.) Scop., *Lactuca serriola* L., and *Arundo donax* L..

No differences in seed density were identified (0.5±10.2 seeds/cm² for transect 1; 0.2±0.05 seeds/cm² for transect 2; 0.3±0.1 seeds/cm² for transect 3; F=0.5, df=2, p=0.6) and species richness (10.3±2.6 species for transect 1; 11.8±1.3 species for transect 2; 9.0±1.7 species for transect 3; F=0.5, df=2, p=0.6) in sticky traps at the different depths.

The dominant species in the sticky traps were the same at each depth: *Lolium rigidum* Gaudin (contributing up to 24% of the total seedling number), *Polygonum aviculare* L. (contributing up to 16% of the total seedling number), *Lactuca serriola* L. (contributing up to 11% of the total seedling number). In the windsock traps, the most dominant species were also *Lactuca serriola* L. (9%) and *Arundo donax* L. (9%).

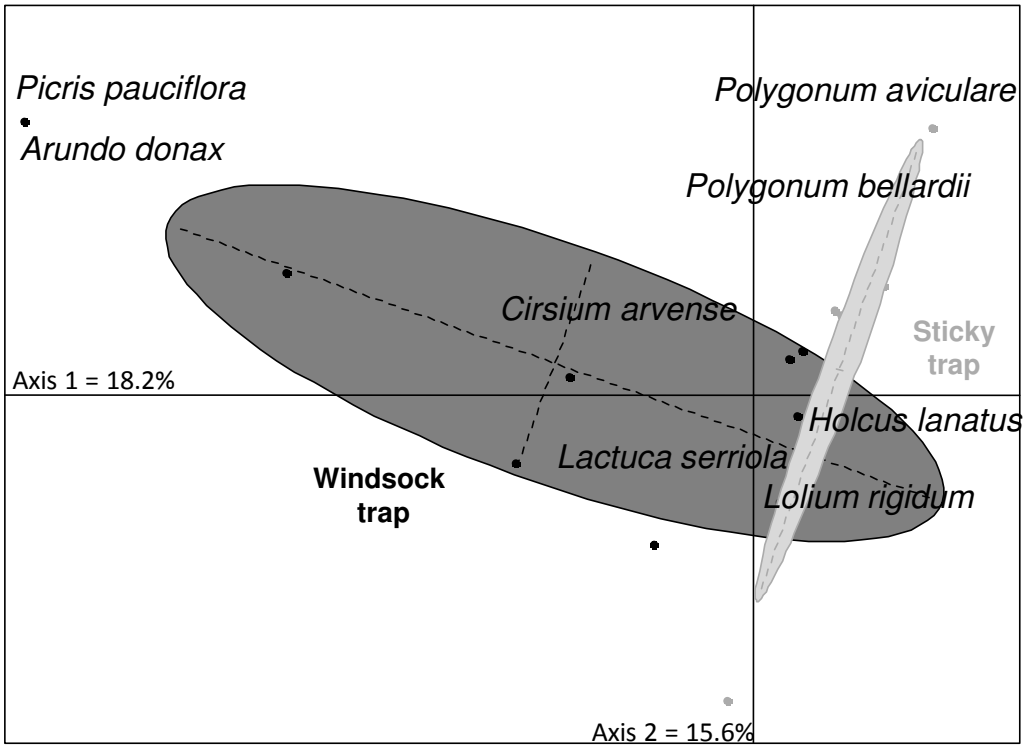


Figure 2.4: Ordination plot of the Correspondence Analysis based on seed density per cm^2 of species (20 plots × 39 species) in windsock traps (black, 8 plots) and sticky traps (grey, 12 plots). In the interest of clarity, only the 7 species with the higher contributions to axis are shown.

2.3.4. Relationships between soil seed bank and seed rain (sticky traps + windsock traps) in terrestrial conditions

Of the 29 species (***Table 2.1***) recorded in the extant vegetation, 12 were recorded in both the soil seed bank in terrestrial condition and in the terrestrial seed rain (sticky traps + windsock traps), 11 were recorded only in the seed rain, 3 were recorded only in the soil seed bank, and 2 species were recorded only in the extant vegetation, and were absent from the seed bank and the seed rain (*Lolium perenne* L. and *Lactuca saligna* L.).

Of the 41 species recorded in the terrestrial soil seed bank, 21 were exclusively found in the seed bank and corresponded mainly to hygrophyte or amphibian species (e.g. *Juncus articulatus* var. *articulates, Cyperus difformis* L., *Ammannia × coccinea* Rottb., *Lindernia dubia* (L.) Pennell, *Typha laxmannii* Lepech) and required particular conditions to germinate. Of the 38 species recorded in the terrestrial seed rain, 10 were found only in the seed rain and corresponded to long distance dispersal species recorded only in the windsock collecting seed with anemochorous dispersal mechanism (e.g. *Arundo donax* L.

and *Picris pauciflora* Willd.), or to grassland target species (*Brachypodium distachyon* (L.) P.Beauv. and *Bromus rubens* L.).

The first axis of the CA (17.2%, ***Figure 2.5***) discriminated the composition of the seed bank from that of the seed rain, with an intermediate position for the extant vegetation.

In the surface, the vegetation composition showed a higher correlation with the composition of seed bank than with that of seed rain (***Table 2.2***). The Spearman correlation coefficient was 0.379 (with *p<0.01)* between the extant vegetation and the seed bank at the surface (transect 1) indicating that species with a higher frequency in the seed bank were likely to be found in the extant vegetation.

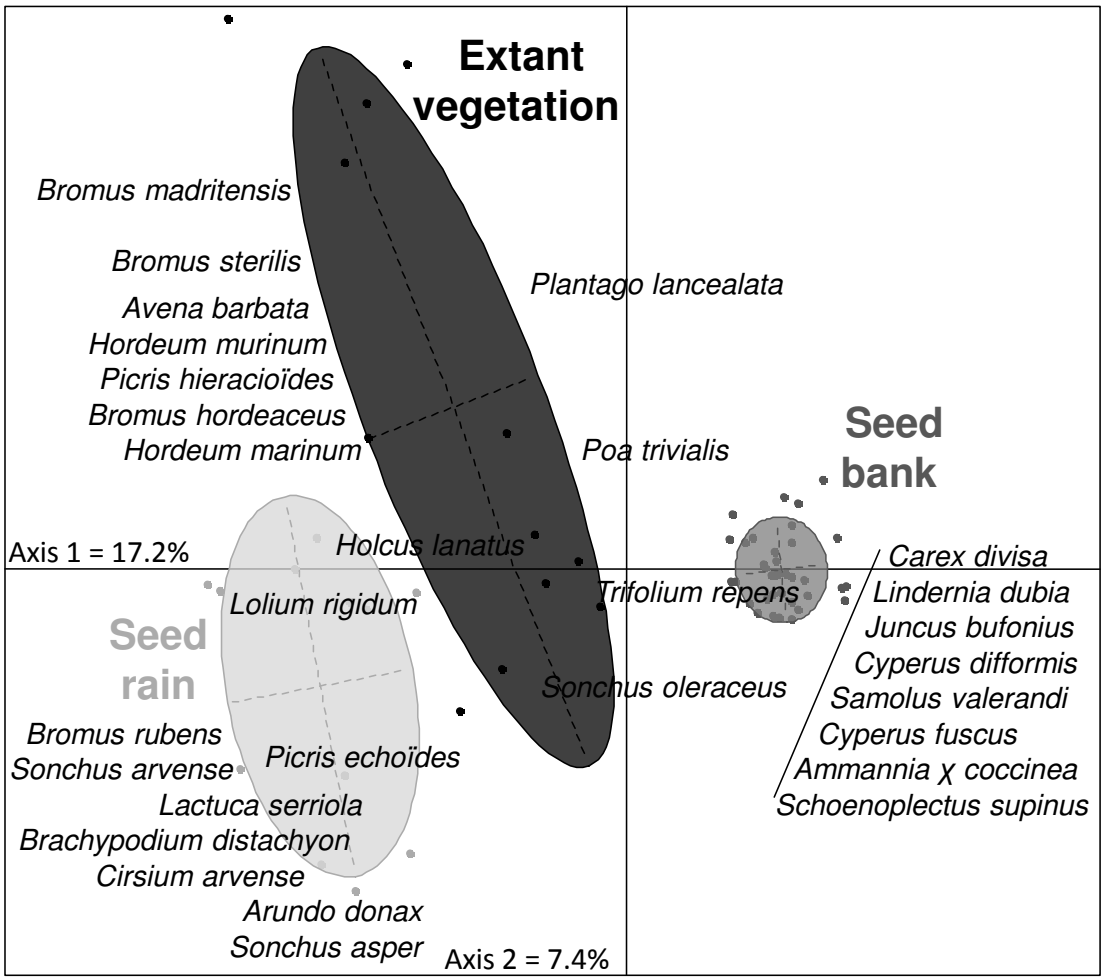


Figure 2.5: Ordination plot of the Correspondence Analysis based on species presence/absence (60 plots × 64 species) on extant vegetation (black, 12 plots), soil seed bank (dark grey, 36 plots), and seed rain (sticky traps + windsock traps, light grey, 12 plots). In the interest of clarity, only the 29 species with the higher contributions to axes are shown.

The trend was reversed with deeper soil removal, where we found a significant relationship between species frequency in the extant vegetation and in the seed rain, with a Spearman correlation coefficient of 0.368 (with *p<0.01).*

Table 2.2: Correlations (Spearman r, with correlation test of significance, and n= number of species) between the frequency of seeds (in the soil seed bank and the seed rain (sticky traps + windsock traps)) and frequency of species recorded in the vegetation at the three depths (NS: non-significant; *: p<0.05; **: p<0.01).

	R	*p*	n
Extant vegetation in surface (transect 1)			
With seed bank	0.379	**	51
With seed rain	-0.008	NS	38
Extant vegetation in 5 cm removal (transect 2)			
With seed bank	-0.190	NS	43
With seed rain	0.100	NS	38
Extant vegetation in 20 cm removal (transect 3)			
With seed bank	0.000	NS	36
With seed rain	0.368	*	39

There was no observable difference in Sorensen similarity index between the extant vegetation and the soil seed bank and the extant vegetation and the seed rain among the different depths (***Figure 2.6***).

At the surface, the similarity index between the vegetation and soil seed bank were significantly higher than with the seed rain (***Figure 2.6***), which is consistent with the correlation coefficient. At the two other depths, the seed bank and seed rain showed an equivalent degree of similarity to the extant vegetation.

Even though a relative discrimination between the seed bank and the seed rain was observed on the CA (***Figure 2.5***), we found relatively high Sorensen indices between these two pools among the various depths, with a significant decrease in transect 2 (***Figure 2.6***).

2.3.5. Relationships among soil seed bank and seed rain (filter and windsock traps) in aquatic condition

On the 12 species (***Table 2.1***) recorded in the extant aquatic vegetation, 1 was recorded in both the soil seed bank in aquatic condition and the seed rain (filter traps and windsocks in the aquatic blocks), 3 were recorded only in the seed rain, 3 were recorded

only in the soil seed bank, and 5 species were only recorded in the extant vegetation, 2 out the 5 were absent from the seed bank and the seed rain of the aquatic blocks (parcel 4) but present in the other parcels and 3 species totally absent from the two other pools of the site (*Cladophora vagabunda* (L.) Hoek, *Phragmites australis* (Cav.) Steud. and *Populus alba* L.).

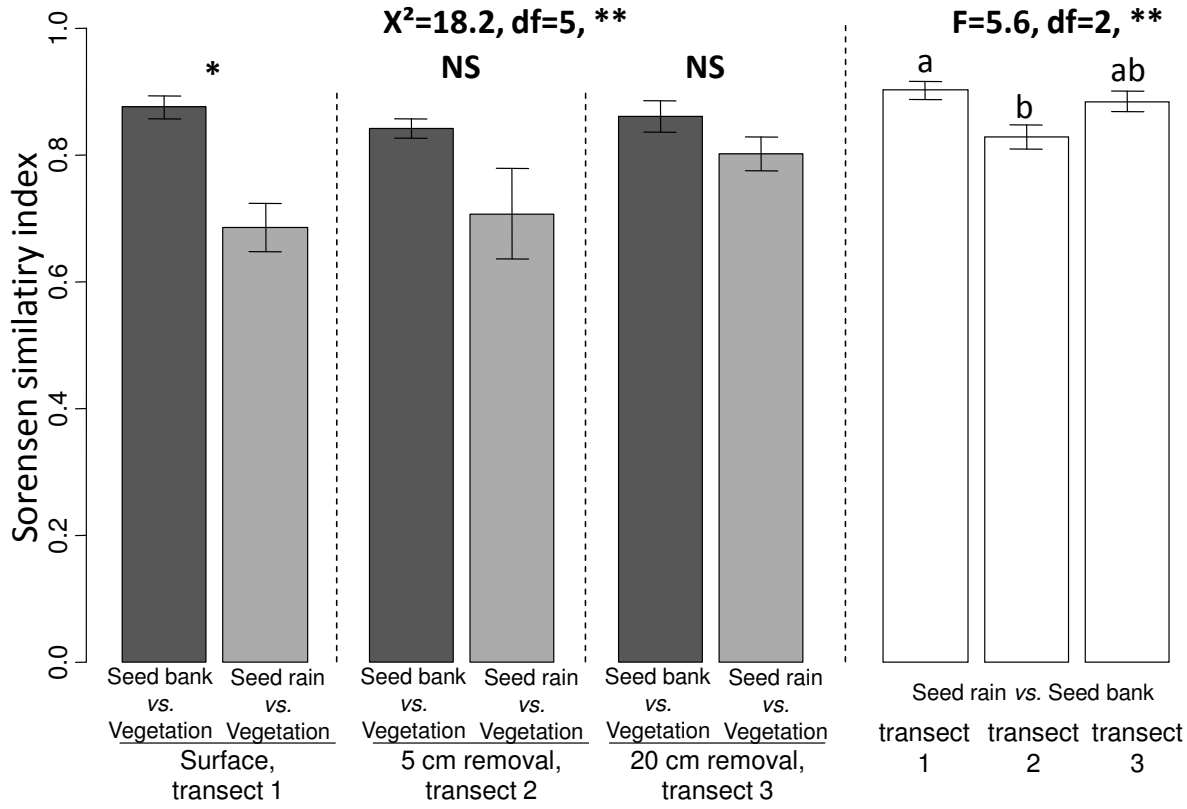


Figure 2.6: Mean and standard errors of Sorensen similarity index based on species presence/absence between extant vegetation and soil seed bank (dark grey, 36 plots), between extant vegetation and seed rain (sticky traps + windsock traps, light gray, 12 plots) and between soil seed bank and seed rain (white, 36 plots) at the three different depths. The F of ANOVA or the χ^2 of Kruskal-Wallis tests performed are shown above the bars (NS: non-significant; *****: $p<0.05$; ******: $p<0.01$), bars showing the same letters do not have any significant differences according to Tukey tests.

Of the 7 species recorded in the soil seed bank in aquatic condition for the aquatic block (parcel 4), 3 were exclusive to this pool, corresponding mainly to hydrophyte or amphibian species (*Chara braunii* C.C. Gmelin, *Cyperus difformis* L. and *Schoenoplectus supinus* (L.) Palla) requiring particular conditions to germinate. Out of the 14 species recorded in the aquatic seed rain (filter traps + windsock traps), 10 were found only in seed rain and corresponded either to terrestrial species recorded in the windsocks (e.g.

Lolium rigidum Gaudin), or to species from the filter traps requiring particular hydrological conditions (e.g. *Lycopus europaeus* L.).

The second axis of the CA (24.9%, ***Figure 2.7***) showed the intermediate position of the extant vegetation between the seed bank and the seed rain. The species frequency in the vegetation was significantly influenced by the species frequency in both the seed bank and the seed rain. The Pearson correlation coefficient was 0.66 (with $p<0.001$) between the vegetation and the seed bank and the Spearman correlation coefficient was 0.75 (with $p<0.001$) between the vegetation and the seed rain.

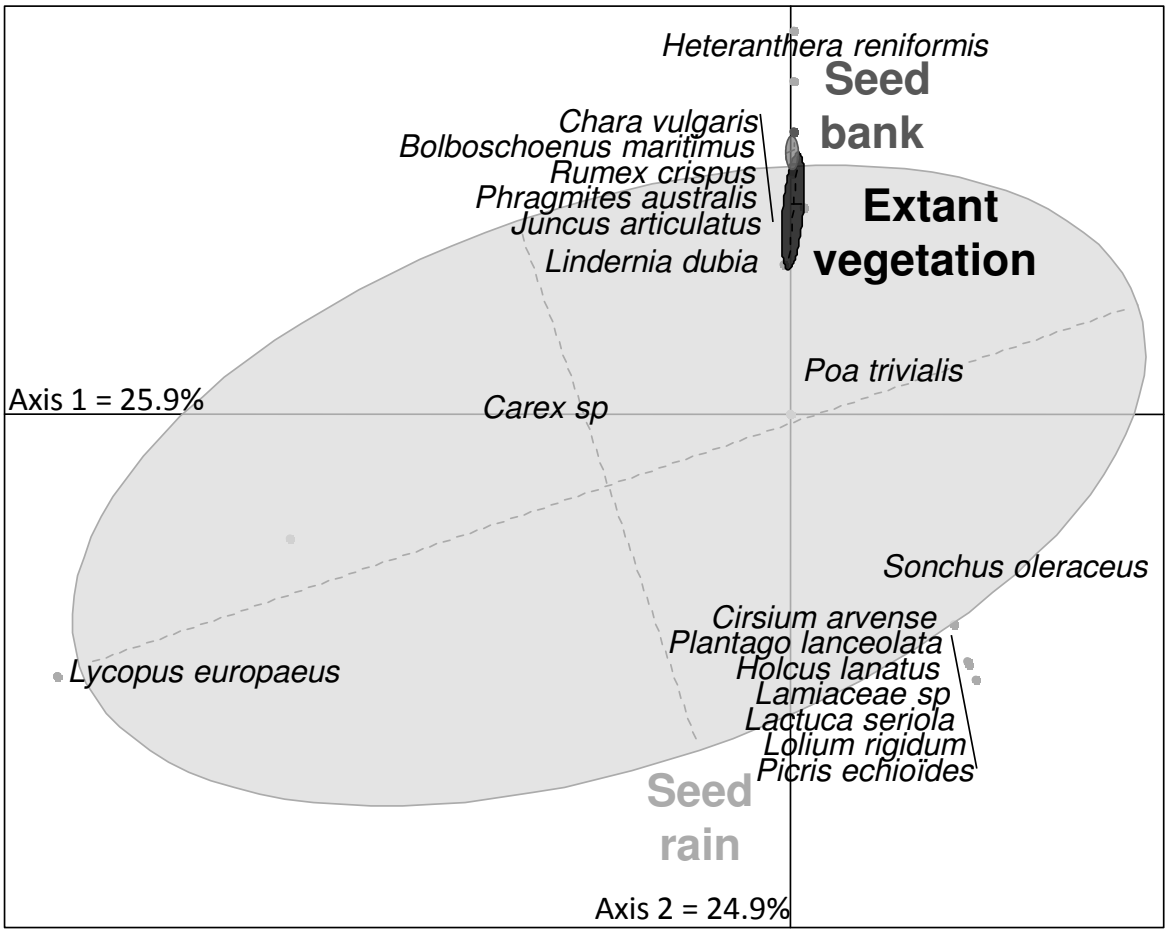


Figure 2.7: Ordination plot of the Correspondence Analysis based on species presence/absence in at least 2 samples (26 plots × 18 species) on extant vegetation (black, 4 plots), soil seed bank (dark grey, 3 plots) and seed rain (filter traps + windsock traps, light grey, 19 plots).

The Sorensen similarity indices confirmed that a strong link exists among the vegetation and the two pools. The index between the seed bank and the extant vegetation was significantly lower than it was between the other pair (***Figure 2.8***).

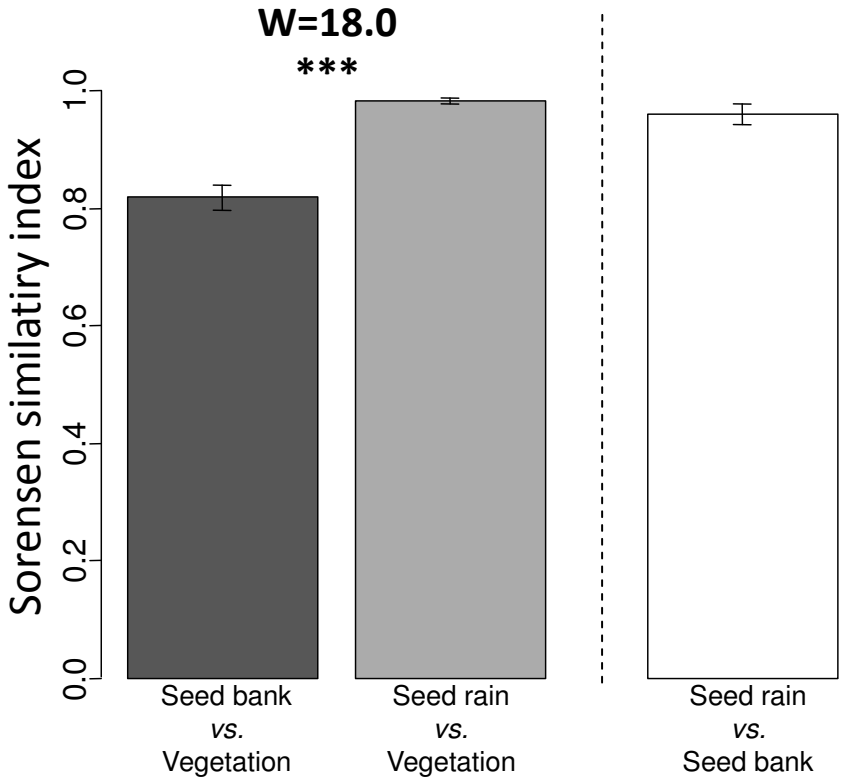


Figure 2.8: Mean and standard errors of Sorensen similarity indices, based on species presence/absence, between extant vegetation and soil seed bank (dark grey, 12 plots), between extant vegetation and seed rain (light gray, 76 plots), and between soil seed bank and seed rain (white, 57 plots). The *W* of Wilcoxon test performed are shown above the bars (***: p<0.001).

2.4. Discussion

2.4.1. Soil seed bank and seed rain

The soil seed bank mainly consisted of exotic ricefield weeds (e.g. *Ammannia* × *coccinea* Rottb., *Heterenthera reniformis* Ruiz & Pav., *Lindernia dubia* (L.) Pennell.), banal ricefield weeds (e.g. *Chara vulgaris* L., *Pulicaria dysenterica* (L.) Bernh., *Schoenoplectus supinus* (L.) Palla), ruderal and nitrophilous species (*Polygonum aviculare* L., *Rumex crispus* L., *Sonchus oleraceus* L.), or meadow species *(Lysimachia arvensis* (L.) U.Manns & Anderb., Plantago major L., Poa trivialis L., Trifolium repens L.), all of which are holdovers from the arable disturbance (deep ploughing regimes, irrigation, and fertilization). These species are known to persist in seed banks in the long term (> 5 years) (Thompson et al. 1997) and may accumulate to high densities in the seed bank (Grime 1979). Topsoil removal of at

least 5 cm appeared to significantly reduce the densities of these seeds. However, no differences were observed between the two deeper (20 cm and 40 cm removal) soil layers. This vertical homogenization of the seed bank densities can be explained by rice cultivation practices, which include a 20 cm deep ploughing. The five target grassland species found in the soil seed bank corresponded to only 1.5 % of the total seedling number. Most soil seed bank studies on degraded sites agree that few species dominate and that typical target species are generally poorly represented (Bakker et al. 1996; Hutchings and Booth 1996; Prach et al. 2001b; Khater et al. 2003; Pywell et al. 2003; Römermann et al. 2005; Buisson et al. 2006b; Török et al. 2011). In our case, we find that seeds of Mediterranean oligotrophic grassland or Mediterranean temporary wetland show an insignificant role in the spontaneous succession processes.

The same conclusion can be drawn for the seed rain; as we found in the terrestrial seed traps, the seed rain is dominated by the same meadow and ruderal species. The five target grassland species found in the seed rain correspond to only 0.8 % of the total seed number. The absence of a difference in seed density and species richness in seed rain sticky traps among the various topsoil removal depths indicates a constant local seed production by the extant vegetation. The discrimination observed between the windsocks and the sticky traps can be explained by the dispersal modes of species. Indeed, species found exclusively in the windsock traps (8 species) corresponded mainly to anemochorous species (e.g. *Picris pauciflora* Willd, *Cirsium arvense* (L.) Scop., and *Arundo donax* L.),while species found only in the sticky traps (17 species) were barochorous (e.g. *Lolium rigidum* Gaudin, and *Polygonum aviculare* L.) and zoochorous (e.g., *Polygonum bellardii* All. and *Holcus lanatus* L) (Stevens 1932). No seeds of the target species can be expected to disperse by hydrochory: the water from the irrigation canal was found to contain only very low numbers of unwanted species, which implies that grassland species and wetland species probably disperse weakly and that the landscape is not favorable to long dispersal mechanisms.

This quasi-absence of target species on site and in the regional species pool can compromise the trajectory of community recovery and of restoration goals by slowing down succession and preventing the establishment of target species (Prach et al. 2001a; Suding et al. 2004). Indeed, four of the target species (out of 28 species in total i.e. 14% of

the total species richness) were recorded on the extant vegetation contributing only 7% of the total abundance. A low density of target species in the seed bank and seed rain can explain the weak contribution to extant vegetation, but unfavorable abiotic conditions could also be playing a role. Topsoil removal only improves abiotic conditions in terms of nutrient availability.

2.4.2. Spontaneous vegetation development

Almost all species recorded in the extant vegetation (in terrestrial or aquatic blocks) emerged from either the seed bank, the seed rain, or both. There were only five species absent from the seed bank and seed rain: *Lolium perenne* L. and *Phragmites australis* (Cav.) Steud., which are perennial species, *Lactuca saligna* L., a biennial species, *Cladophora vagabunda* (L.) Hoek, a green filamentous algae whose dispersal is mediated by less than 100 µm-diameter spores (not captured with our methodology), and *Populus alba* L., an anemochorous species. This absence of species in seed rain and seed bank can therefore be explained by plant strategy (the probability of seed detection is smaller for perennial or biennial species) and by methodological bias in trapping seeds.

Information concerning species absent from the extant vegetation and present in seed rain is crucial to seed availability and plant succession. Moreover, one of the effects of topsoil removal is to create bare unsaturated soil allowing a better recruitment of seeds (Greene and Johnson 1989). Also, long-distance dispersal mechanisms, despite the fact that they are rare events, may sometimes play an important role in plant community assembly (Soons et al. 2004; Soons and Ozinga 2005). In our study, no target species with long dispersal mechanisms were identified. The 13 species absent from the extant vegetation and present in the seed rain are either anemochorous species, which propagate via long dispersal mechanisms and do not meet the required conditions to grow, or hydrochorous species, which require spring inundation to germinate (e.g. *Heterenthera reniformis* Ruiz & Pav.). Our vegetation monitoring did not cover the global extant vegetation. Concerning the 22 species absent from the extant vegetation but present in soil seed bank, germination requirements and conditions for their growth were not being met (e.g. hydrophyte species).

We observed a high Sorensen similarity index between the extant vegetation and the seed bank and the extant vegetation and the seed rain. In the terrestrial blocks, the similarity index between the extant vegetation and the seed bank was significantly higher than it was between the extant vegetation and the seed rain (at least on the surface). The exact opposite was true of the aquatic blocks. The extant vegetation was influenced both by the seed bank than by the seed rain, but it was also a contributor to the seed bank and seed rain through short-distance dispersal mechanisms, and this led to a high similarity index between the seed bank and seed rain in both aquatic and terrestrial conditions. However, while the aquatic blocks exhibited high correlation coefficients between the extant vegetation and both seed rain and seed bank, the terrestrial blocks showed significantly more correlation between the extant vegetation and the seed bank in the surface and in the deeper-layer between the extant vegetation and seed rain. Our hypotheses that the seed rain influences the vegetation more strongly when soil is removed from deeper depths, and that the seed bank contributes more to recruitment in the upper layers, were supported. Topsoil removal appears to reverse the effect of seed bank and seed rain on vegetation. By successfully removing half of the seed bank and offering unsaturated sites, soil removal allows seed rain to play a more important role in vegetation. Topsoil removal offers a greater opportunity for long-distance dispersal events and plant community changes.

2.4.3. *Mediterranean oligotrophic grassland vs. temporary wetland ecosystem restoration*

In wetland ecosystems, abiotic filters are easier to control by water management than they are in terrestrial grasslands. From this it follows that the abiotic conditions in aquatic ecosystems are easier to restore, and that they lend themselves to better predictions of the community and to more complete plant restorations. As Zedler (2000) correctly stated, "it takes more than water to restore a wetland;" nevertheless, the hydrological filter has an important selective effect and only aquatic species can survive in such an environment. This does not mean that with wetland ecosystems, spontaneous succession process will always be successful. Rather, it indicates that it would potentially be easier to restore Mediterranean temporary wetland than Mediterranean oligotrophic

grassland in the wake of the same type of agricultural disturbance. Indeed, restoring oligotrophic grassland communities on degraded sites having a nutrient-enriched soil and a seed bank dominated by ruderal species makes the establishment of nutrient-poor, low-competitive, and stress-tolerant species more complicated. Even though topsoil removal does decrease soil nutrients (***Chapter 3*** and ***Chapter 4***) and seed density in the soil seed bank, it does not result in the restoration of the abiotic conditions of oligotrophic grassland, and the community is more subject to negative biotic interactions because grassland target species have to compete with dominant ruderal and common meadow species coming from the site's agricultural past (Kiehl et al. 2006).

Prach and Hobbs (2008) confirm this by advocating the use of spontaneous succession only when environmental site conditions are not very extreme and easy to restore. They attest that the probability of attaining a target stage by spontaneous succession decreases toward both ends of the productivity–stress gradient, whereas technical measures increase it.

2.4.4. Perspective of vegetation restoration

Dispersal is crucial for metapopulation dynamics, re-colonization of sites, and establishment of new populations. The environmental conditions of a site represent an important variable determining the rate and direction of vegetation colonization, but at the same time, suitable abiotic conditions do not necessarily guarantee the successful restoration of an ecosystem. Dispersal may be the limiting factor for plant colonization and re-establishment. Thus, the landscape matrix (Prach and Pysek 2001) and connectivity (Bedford 1996; Bornette et al. 1998) can strongly influence the type of succession. Řehounková and Prach (2007) showed that landscape factors can explain more vegetation variability than do local site factors. A fragmented landscape creates dispersal limitations by increasing the distance between populations, until it becomes greater than the dispersal ability of the species, with the end result that the long-term survival of the species is threatened unless dispersal ability can be re-established (Trakhtenbrot et al. 2005). The preference for spontaneous succession is generally more manifest when the site to be restored is surrounded by the undisturbed target ecosystem (Prach and Pysek 2001; Suding et al. 2004; Prach and Hobbs 2008). A more isolated site has less of a chance

to be colonized by target species and may be colonized by stronger recolonizers capable of preventing the establishment of diverse native plant communities (Prach et al. 2001b).

In this study, not all types of dispersion were recorded. Indeed, the importance of seed dispersal by large animals, something we have not considered, has been described elsewhere (Fischer et al. 1996). Livestock can act as excellent vector for dispersing the seeds of grassland species, and a fraction of Mediterranean oligotrophic species are known to be epizoochorous (Stevens 1932). The same conclusion can be drawn for Mediterranean temporary wetland species, in which zoochorous dispersal by waterbirds plays a major role in colonization (Figuerola and Green 2002a; Brochet et al. 2010a). All of these facts suggest that our seed rain study may have underestimated the number and effect of real plant dispersal mechanisms. Moreover, a variety of different traps was used in estimating seed rain. However, because the sampling pressure was different between the windsocks and the sticky traps, the species richness estimates provided by the sticky traps were biased as a result of the sticky traps' larger sampling area. The bias was evident even when we attempted to consider areal density (seeds per cm^2). In addition to the differing sampling pressures, the soil seed bank was recorded using the seedling emergence method, which only counts viable seeds, while seed rain was estimated by the total number of seeds with no consideration of viability. But, the question of seed viability is much more important for the soil seed bank, in which a variety of seed ages are mixed, than in seed rain, which is essentially a sample of only recent production in which seeds are in better condition overall.

In the end, the extant vegetation, seed rain, and soil seed bank results suggest clearly that our ability to restore the grassland or wetland plant community on abandoned fields using a passive restoration approach is largely ineffective. The regional pool species is not a potential source of recruits from the target species, so active restoration is advisable for wetland (***Chapter 3.1***) and grassland ecosystems (***chapter 4***). Indeed, seed addition using hay transfer (e.g. Hölzel and Otte 2003; Klimkowska et al. 2010b) or soil transfer (Valk et al. 1992; Brown and Bedford 1997) have been shown to be effective measures for overcoming this apparent limitation of grassland or wetland ecosystems. Our result suggests that seed rain is more important for the plant community at the deeper depths,

indicating that transfer, simulating seed rain, combined with topsoil removal, can be useful for changing a plant community.

Community assembly may be a function not only of dispersal processes, but also of local interactions among species post-recruitment. Indeed, early community development is strongly influenced by seed availability, and in the later stages of vegetation development, the role of internal community processes increases (Lepš 1999; Hobbs and Norton 2004; Standish et al. 2008; Baer et al. 2009). Performing active restoration in the early stages of vegetation development may produce better results, because communities are less influenced by biotic interactions, and species are more able to establish in unsaturated sites as the present study suggests.

Transition to Chapter 3

In ***Chapter 2***, we show that even after the restoration of abiotic conditions, spontaneous succession is unlikely to lead to Mediterranean meso-xeric grassland and temporary wetland ecosystems. Species introduction is therefore needed to try to recover ecosystems (Hölzel et al. 2012). If we manipulate the abiotic and the dispersal filter, can we restore the plant community? Are responses to species introduction different between the aquatic and the terrestrial ecosystem? Does a positive response to plant community also reveal positive responses in another compartment? These questions are tackled in ***chapter 3*** and ***Chapter 4***, involving the same small-scale experiment than in the ***chapter 2***, where restoration techniques were used, and were different components were monitored.

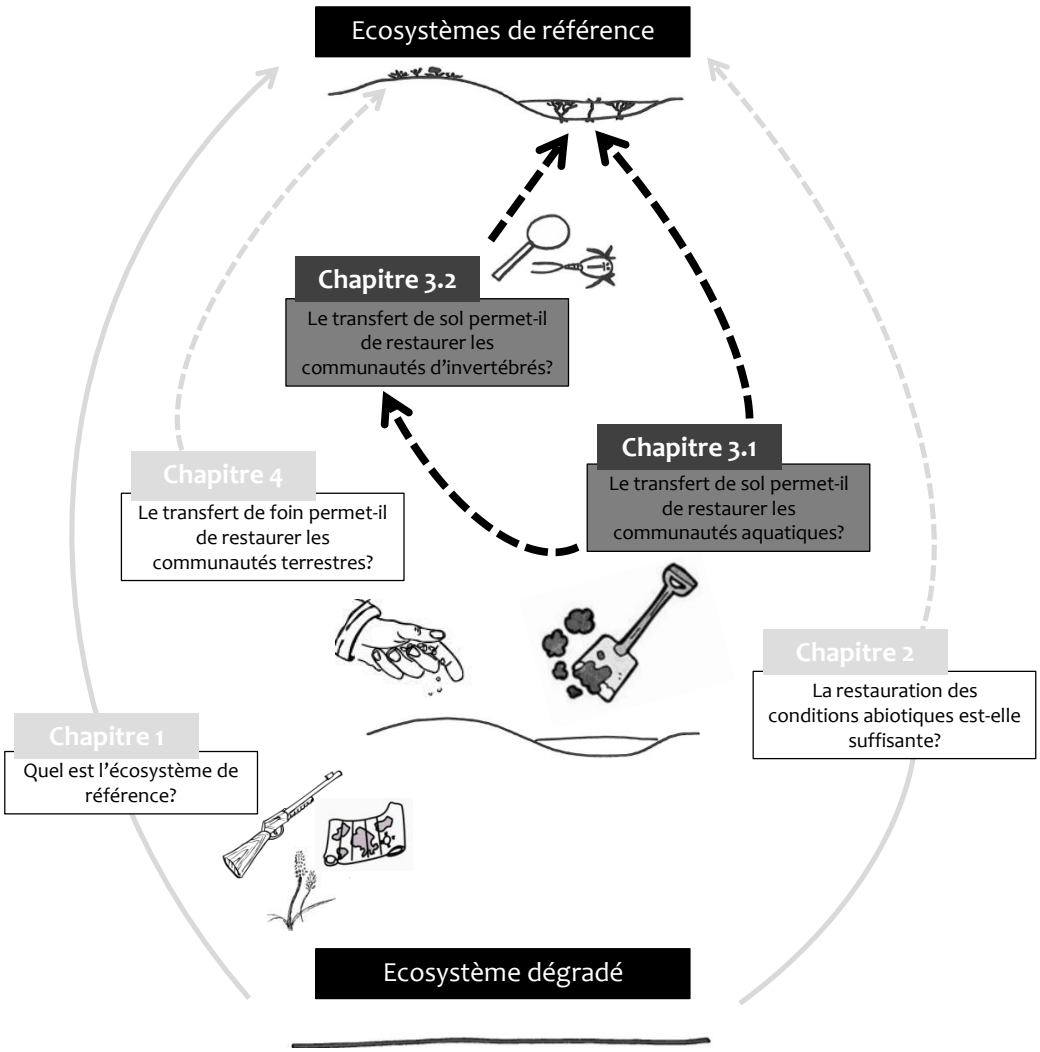


Figure T3.1: Location the ***Chapter 3.1*** and ***Chapter 3.2*** in the general thesis organization

Soil collecting in a temporary wetland during the summer.

Aquatic invertebrates sampling in an experimental block.

Aquatic vegetation monitoring after soil transfer in an experimental block (*Ranunculus peltatus*).

Chapter 3 – Creation of Mediterranean temporary wetland using soil transfer

Section 3.1: Temporary wetland restoration after rice cultivation: is soil transfer required for aquatic plant colonization?

Isabelle Muller, Elise Buisson, Jean-Baptiste Mouronval, François Mesléard

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3.1.1. Introduction

The remaining global extent of wetlands is estimated to be over 1.2 million square kilometers. During the twentieth century, in North America, Europe, and Australia more than 50% of certain types of wetlands were destroyed (Millennium Ecosystem Assessment 2005). Due to this wetland loss, many countries have implemented specific regulations to protect wetlands (e.g. the US "clean water act" of 1972 (McMahon Jr 1972) or the European Water Framework Directive of 2000 (European Commission 2000)). These regulations include restoration and conservation of water integrity by limiting pollution and maintaining the overall integrity of wetlands. Indeed, wetlands provide multiple ecosystem services, such as water purification and waste water treatment, regulation of hydrological flow, climate and erosion, primary production, and biodiversity conservation (Zedler and Kercher 2005; Millennium Ecosystem Assessment 2005). Therefore, in recent decades, wetland restoration (Society for Ecological Restoration 2004) has received increased attention (Zhang et al. 2010).

In the Mediterranean Basin, wetlands have been greatly impacted because they are particularly productive systems which were converted for agriculture and tourism (Hollis 1992). The remaining wetlands are of important ecological, social and economic values (Grillas et al. 2004). Natural temporary wetlands of the region are characterized by winter and spring flooding, with durations that greatly vary from year to year, and by a complete drying-out in summer (Grillas et al. 2004). They represent one of the most remarkable Mediterranean habitats, comprising a high plant diversity of particularly annuals species (some of which are rare and endangered) adapted to the specific climate (i.e. necessity to be annual species to support the dry summer with short favorable periods for reproduction), such as *Zannichellia obtusifolia* Talavera & al*, Callitriche lenisulca* Clavaud or *Tolypella hispanica* T.F. Allen (Grillas and Duncan 1986; Grillas et al. 2004). During the 20th century, temporary wetlands were subject to degradation and drastic area reduction in the Mediterranean region due to agriculture, industry, recreational activities, and hunting (Hollis 1992; Grillas et al. 2004). One of the main causes of the degradation of Mediterranean temporary wetlands is the water management for hunting activities that maintains the water level in spring and/or in summer and that has led to a decline of plant communities that are restricted to temporary wetlands along with an increase in

perennial and cosmopolitan species (Tamisier and Grillas 1994; Aznar et al. 2003). Mediterranean temporary wetlands are thus considered a priority habitat (code 3170) according to the Natura 2000 Network of the European Union Habitats directive (European Commission 1992). Wetland restoration (Society for Ecological Restoration 2004) is urgently needed to stop the loss of this habitat type. In order to restore a wetland, two strategies can be adopted to establish plant communities: i) one based on spontaneous succession with recruitment from residual seed bank or from seed dispersal, or ii) active restoration which requires propagule introduction.

Spontaneous colonization may provide satisfying results in terms of plant composition and may also promote wetland "self-design" capacity as a response to hydrological conditions (Mitsch et al. 1998; Prach et al. 2001a). If the appropriate environmental conditions, mainly consisting of flooding regimes, water depth, and salinity, are restored (Grillas 1990), vegetation can rapidly establish from the residual seed bank (Leck 2003; De Steven et al. 2006). Short distance dispersal (Reinartz and Warne 1993), long distance endozoochorous (Zedler and Black 1992; Figuerola et al. 2002; Brochet et al. 2010b), and ectozoochorous (Figuerola and Green 2002b) dispersal may also contribute to spontaneous colonization. Active revegetation methods may not be needed if sources populations of desired seeds are available nearby and if physical barriers do not hamper dispersal (Moreno-Mateos and Comin 2010).

Vegetation recovery is often limited by a low density and a high distance of seed sources (Bischoff 2002). Several studies have demonstrated dispersal limitation despite the proximity of natural temporary wetlands (Galatowitsch and Valk 1996; Collinge and Ray 2009). Moreover, the site to be restored may be isolated from the network of wetlands (Reinartz and Warne 1993; McKinstry and Anderson 2005) or may have been submitted to a long cultivation period (Prach et al. 2001b), which often limits re-colonization. In such cases, active restoration, including reestablishment of dispersal vectors, is needed to restore plant communities (Bischoff 2002). Community translocation involves the removal of the full species assemblage of a site and the establishment of a functioning community at a new receptor site (Bullock 1998). Transfer of bulk soil is such a community translocation method. It is often used in wetland restoration and has already shown promising results: the imported soils contribute

considerably to species richness and native wetland species establishment, indicating that soil transfer may enhance the success of wetland restoration projects compared to natural colonization (Reinartz and Warne 1993; Balcombe et al. 2005a; Nishihiro et al. 2006). Moreover, this technique could be the most efficient method for transferring a large number of temporary wetland plant species that have a short life cycle but can produce large quantities of seeds and rapidly form a large seed bank (Mouronval and Baudouin 2010).

In the present study we investigate the benefits of soil transfer when compared to spontaneous succession in temporary wetland restoration of former ricefields. Before testing spontaneous colonization *vs.* active revegetation, physical manipulations need to be included, e.g. hydrological and topography restoration, in particular if environmental conditions are not appropriate. This is often the case if the wetland has been destroyed for cultivation, resulting in strong modifications of the former topography and of the inundation periods. Only after restoration of abiotic conditions, the potential of spontaneous colonization can be evaluated. We thus used experimental on-site wetland blocks to address the following questions: (1) is spontaneous succession sufficient to restore typical Mediterranean wetlands on former ricefields? (i.e. what can we expect from the seed bank of former ricefields considered as wetland?); (2) does soil transfer accelerate the colonization of target species and does it increase species richness and the abundance of wetland plants?; (3) is soil transfer required if the site to be restored is close to natural wetlands?

3.1.2. Materials and methods

3.1.2.1. Study site

The experiments were conducted at the Cassaïre site (c. 43°31' N, 4°44' E, 3 meter maximum elevation) located east of the Camargue area (Rhône delta, Southern France, ***Figure 3.1.1.A***) with an average substrate salinity of 0.22 g/L. The climate is typically Mediterranean, characterized by an annual average temperature of 15°C, an annual rainfall of 550 mm mainly concentrated in autumn, and a summer drought. The site has been submitted to recurrent leveling for rice cultivation since the 1940s, eliminating the

natural topography. Cultivation definitively stopped in 2004. On the old Cassini map dating from the eighteenth century, the site was marked as a wetland, and the final aim of the restoration project is to create 35 hectares of Mediterranean temporary wetlands with native aquatic flora including the rare and endangered species found nearby in the Camargue area. The objective of the present study was to identify methods that may also used in large scale restoration projects. The experiments were set up in 2011.

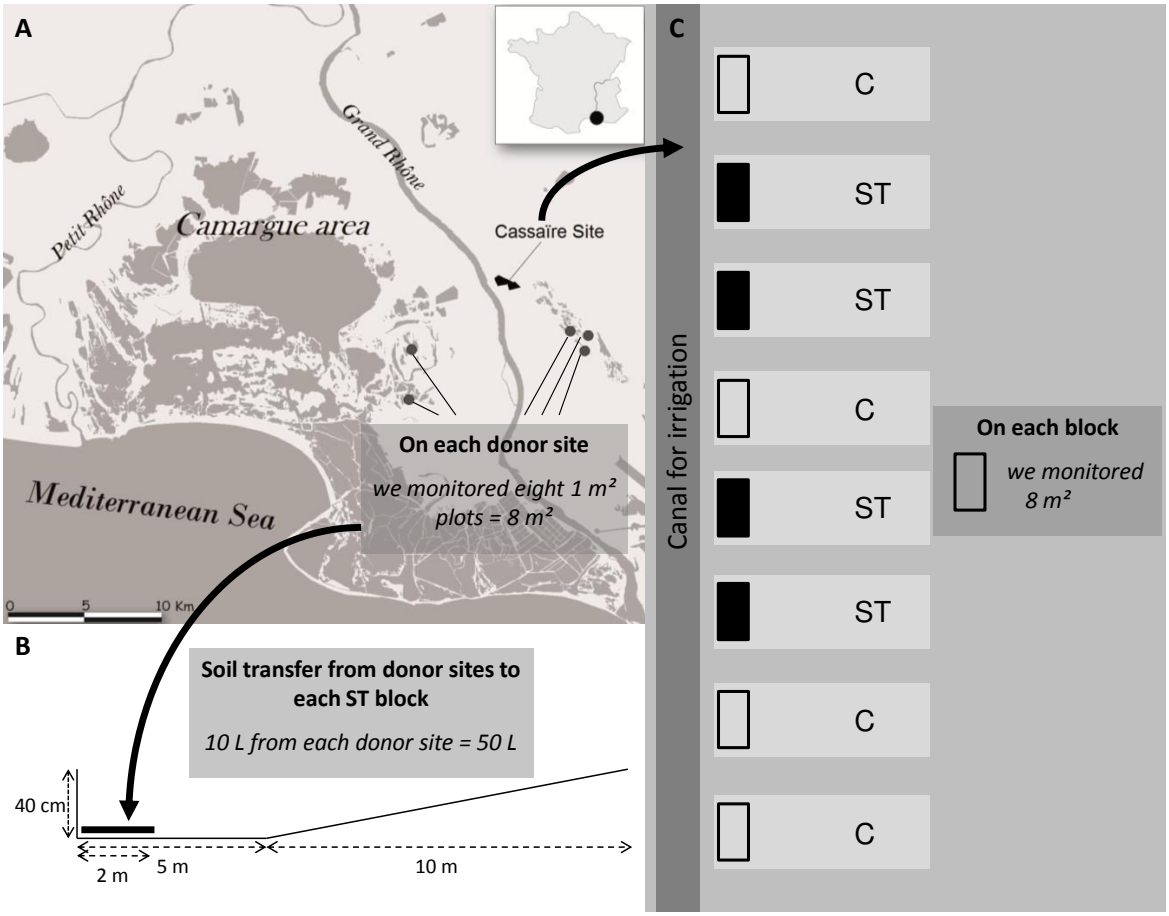

Figure 3.1.1: Location of the Cassaïre site (in black) and of the five donor sites (grey circle). The light grey shading indicates the wetlands of the Camargue area (A). Side view of one soil transfer block (B). Experimental design of restoration treatments at Cassaïre site (C). C = control blocks and ST = soil transfer blocks (black rectangle indicates the soil transfer).

3.1.2.2. Donor sites

In order to maximize the number of locally adapted aquatic plant species at the Cassaïre site, we selected five temporary wetlands as donor sites in the surroundings (between 1 and 6 km, ***Figure 3.1.1.A***) resulting in an inventory of plant communities and abiotic conditions of all the temporary wetlands of the Camargue area. The environmental conditions of these five donor wetlands corresponded to the range of

expected environmental conditions at the Cassaïre site after the creation of the temporary wetland: i.e. having a flooding period from September to June only, a maximum water depth of 40 cm, and a salinity below 6 g/L. Not all the target hydrophyte species were found in a single donor wetland but the five donor sites together represent the regional target hydrophyte species pool quite well. We attempted to select the most appropriate species to the different abiotic filters in the Cassaïre site driven by the environmental conditions of our recreated wetland. Indeed, plant communities of temporary Mediterranean wetlands vary with salinity, hydroperiod, depth, so we maximized the pool of species, allowing the most suitable species to grow in the environmental conditions of the Cassaïre site.

In March and May of 2011 (representing vernal and late season vegetation; (Grillas et al. 2004), we analyzed the vegetation in each of the five donor sites. In each site, we placed eight 1 m^2 plots covering the full humidity gradient. In each plot, we recorded the total percent cover of aquatic vegetation and the cover of each species using a modified Braun-Blanquet scale (Braun-Blanquet et al. 1952): 0.5 for species covering less than 1%, 1 for species covering between 1% and 5% of the plot, 2 between 5% and 25%, 3 between 25% and 50%, 4 between 50% and 75% and the coefficient 5 for species covering more than 75% of the plot. In August 2011, during the dry period when all plants are dormant as seeds in the seed bank, we collected per donor site 45 × 45 cm to a depth of 3 cm soil samples in each plot (eight soil samples in total per donor site), resulting approximately in a total of 40 L of soil per donor site. Our assumption was that these collected soils would contain the seeds of the species recorded in the plots a few months earlier. We pooled the 8 samples of each donor site to one bulk sample using a cement mixer and we stored them under dry until the transfer to the Cassaïre site.

3.1.2.3. Block experiments and soil transfer

To simulate the suitable environmental conditions of a Mediterranean temporary wetland, eight blocks with a gentle slope were dug out (15 m long × 5 m large × 40 cm deep; ***Figure 3.1.1.B***) along a canal that was used for irrigation. Four blocks were used to test soil transfer. The four other blocks were used as control to monitor spontaneous vegetation establishment. The position of treatments was randomized (***Figure 3.1.1.C***). We

pooled 10 L samples from each of the five sites and we spread this 50 L of soil on a 4 × 2 m plot at the bottom of each transfer block (***Figure 3.1.1.B***). A pump maintained a constant 20 cm water level from the day after the transfer in January 2012 (inundation beginning four months after classical temporary wetland conditions but allowing even so the vernal species germination in March) to the end of May 2012. Mid-May to mid-June corresponds roughly to the local dry out of temporary wetlands.

3.1.2.4. Vegetation monitoring

Our aim was to compare soil transfer with control plots in term of similarity to the donor sites. Vegetation monitoring was carried out in May 2012 (four months after the transfer), when most species show their biomass peak. For each of the block 4 m × 2 m plot (8 m²; ***Figure 3.1.1.C***), we estimated the total cover of aquatic vegetation (%) and the cover of each species using the same method as for the donor sites of the previous year. Area of the donor site vegetation analyses was adjusted to that of the block plots (8 m²) by pooling the eight 1 m² plots of each donor site.

Among all plant species occurring in the experiment (***Table 3.1.1***), we assigned aquatic species to one of the following categories:

1. Target hydrophyte species: Present at donor sites according to the classification of temporary wetlands (Grillas and Duncan 1986), corresponding to the native or typical flora of the temporary wetlands of the Camargue area, adapted to the Mediterranean climate, with protection status and threatened by some types of water management, such as fresh water production in the summer (*Callitriche* sp., *Callitriche truncate* Guss., *Chara aspera* C.L. Willdenow, *Chara canescens* A. Langangen, *Chara globularis* J.L. Thuiller, *Ranunculus peltatus* Schrank, *Ranunculus trichophyllus* Chaix, *Tolypella glomerata* (Desvaux) Leonhardi, *Tolypella hispanica* T.F. Allen, *Zannichellia obtusifolia* Talavera & al *and Zannichellia pedicellata* Wahlenb. & Rosèn).

2. Ricefield hydrophyte weeds: Present with rice cultivation (Marnotte et al. 2006). Ricefield weeds are often exotic species introduced by rice cultivation (*Lindernia dubia* (L.) Pennel) but can also correspond to banal algae enhanced by rice water management (*Chara vulgaris* L.), and therefore associated with eutrophic and flooded summer

wetlands. These widespread algae may occur in the reference ecosystems, but cannot be considered as target hydrophyte species.

3. Green filamentous algae: Occurring in temporary wetlands at high temperatures and high nutrient levels (*Cladophora vagabunda* (L.) Hoeck and *Spirogyra* sp.)

Table 3.1.1: Species occurring in blocks, in donor sites and target hydrophyte species.

Species recorded in blocks	Species present in donor sites	Aquatic target species
Atriplex hastata	×	
Bolboschoenus maritimus	×	
Callitriche sp.	×	×
Callitriche truncata	×	×
Carex divisa		
Chara aspera	×	×
Chara canescens	×	×
Chara globularis	×	×
Chara hispida	×	
Chara vulgaris	×	
Cladophora vagabunda	×	
Crypsis aculeata	×	
Juncus maritimus	×	
Lindernia dubia		
Phragmites australis	×	
Poa trivialis		
Potamogeton pectinatus	×	
Ranunculus peltatus	×	×
Ranunculus trichophyllus	×	×
Rumex crispus		
Scirpus littoralis	×	
Sonchus oleraceus		
Spirogyra sp.		
Tolypella glomerata	×	×
Tolypella hispanica	×	×
Typha laxmanii		
Zannichellia obtusifolia	×	×
Zannichellia pedicellata	×	×

All the target hydrophyte species and ricefield hydrophyte weeds are annual species, produce large quantities of seeds that survive several years and are very resistant to drought (Marnotte et al. 2006; Mouronval and Baudouin 2010). However, for some Characeae (*Chara globularis* and *Chara vulgaris*) as well as the two ranunculus (*Ranunculus*

peltatus and *Ranunculus trichophyllus*), plants can be annual or perennial. The Mediterranean climate with temporary wetlands selects the annual nature of these species, perennials do not tolerate the summer dry season.

3.1.2.5. Soil nutrients

To compare soil conditions between the Cassaïre and the donor sites, the following soil properties were measured by the soil analysis laboratory of the INRA (The French National Institute for Agricultural Research, Aras, France): organic matter, total C, total N, P_2O_5, pH and conductivity. Before setting up the block experiment, five soil samples, composed of one liter of soil, were taken from the surface (0-10 cm) and from 40-60 cm depth (corresponding to the digging depth of the block i.e. the new soil surface). In each sample, three sub-samples were taken at random and subsequently pooled for analysis. The same method was applied to the five donor sites (one sample from the surface (0-10 cm) comprising three sub-samples per donor site) to obtain a reference for the soil nutrient status in the target communities. Samples were dried and sieved (to 200 µm).

3.1.2.6. Data analysis

We used different factorial and multivariate analyses to compare transfer and control blocks with donor sites. Contrary to the position of soil transfer and control within the block experiment, the position of donor sites and Cassaïre site is not randomized. We still include donor sites and block treatments in the same models because we are convinced that environmental conditions are very similar and that we can use donor sites to characterize the target community of restoration.

In order to compare soil data between the donor sites and the Cassaïre site, and to assess the habitat suitability of the Cassaïre site, we performed a Principal Component Analysis on soil nutrient contents (15 samples × 6 variables).

To analyze differences between control and soil transfer, we used nonparametric multivariate analysis of variance (nonparametric MANOVA) (Anderson 2001). We used Bray-Curtis similarity index (Raup and Crick 1979) with 999 permutations based on species coefficient cover to compare the species composition. We also performed a Correspondence Analysis (CA) on the vegetation data of the donor sites, of the transfer

blocks, and of the control blocks (13 plots × 28 species). In order to characterize the success of the soil transfer, we calculated the Bray-Curtis similarity index. For each plot surveyed in a block, the mean Bray-Curtis index between this plot and the 5 plots surveyed in donor sites (one per donor site corresponding to an average of the eight 1 m^2 plots per donor site) was calculated. In order to assess donor site variability, we compared the plot of each donor site to that of the other donor sites, obtaining also a mean Bray-Curtis similarity index for donor sites.

We compared the means of the soil nutrient variables, the species richness, the total cover of aquatic vegetation, the means of the Bray-Curtis index and the plant species categories (i.e. target hydrophyte species, ricefield hydrophyte weeds and green filamentous algae) between soil transfer, control and donor sites using a one-way analysis of variance (ANOVA), followed by Tukey post-hoc tests (Sokal and Rohlf 1995) if the data met the assumptions of ANOVA. If data did not comply with assumptions, we performed Kruskal-Wallis and pairwise Wilcoxon tests with a p-value adjustment according to the simple Bonferroni method, in which the *p*-values are multiplied by the number of comparisons.

All tests were performed using R 2.12.0 (R Development Core Team 2010) with a p=0.05 threshold using "ade4" package (Dray et al. 2007) and "vegan" package (Oksanen et al. 2008).

3.1.3. Results

3.1.3.1. Soil nutrients

The soil found at a depth of 40-60 cm on the Cassaïre site became surface soil in the redesigned wetland topography (future soil surface), and it differed from the existing surface soil in Cassaïre and from that of the donor sites (***Figure 3.1.2***). P_2O_5 content was significantly higher in the Cassaïre current surface soil, while pH was significantly higher in Cassaïre deep soil layer. The other nutrients, organic matter, total C, total N, and conductivity were significantly higher in the donor site soils.

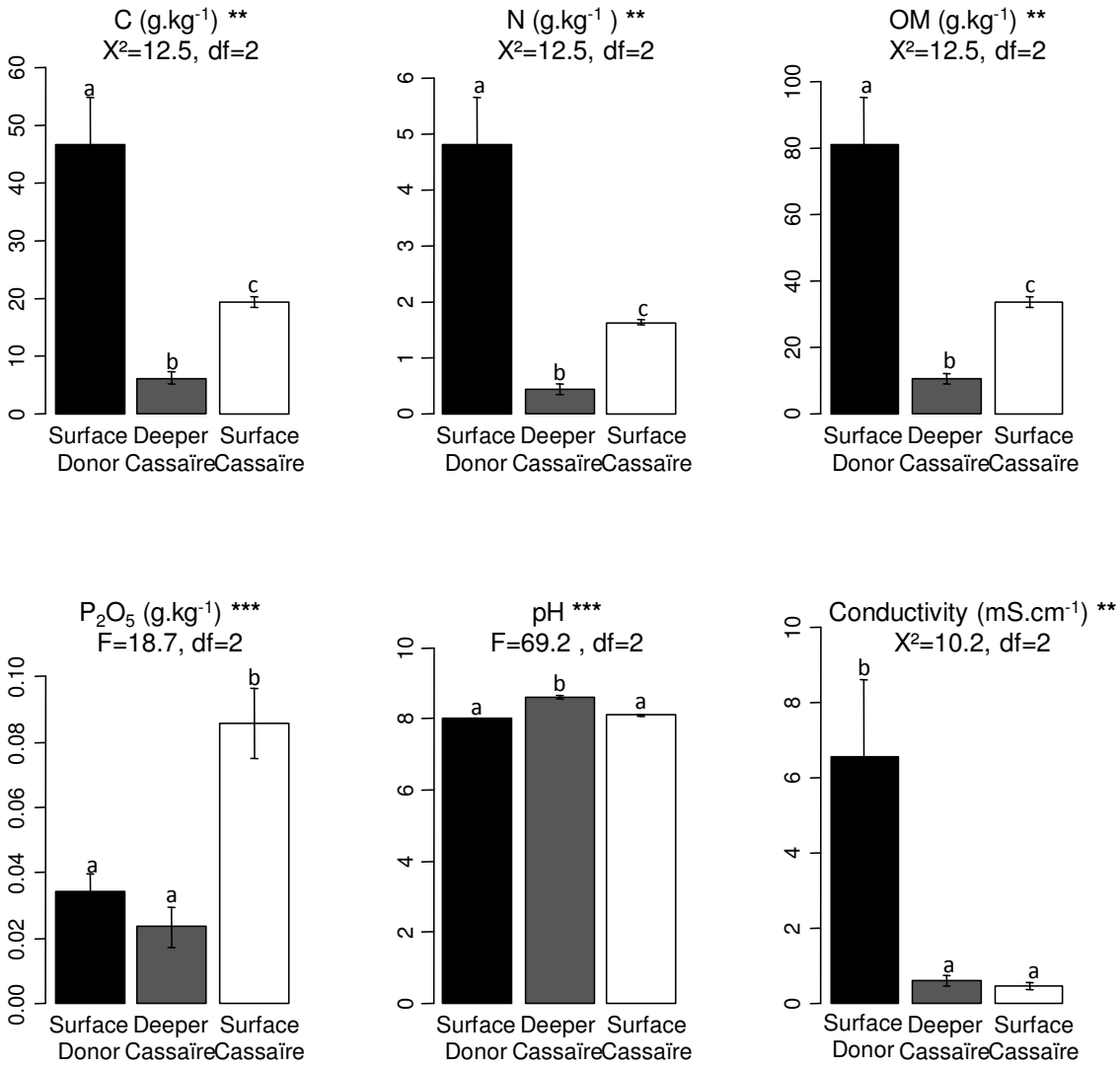

Figure 3.1.2: Mean values ± standard errors of total Carbon (C), total Nitrogen (N), Organic Matter (OM), Phosphorus (P2O5), pH and Conductivity in the surface soil of the donor sites (black bars, n=5), in the surface soil of the Cassaïre site (current soil surface; white bars, n=5) and in the deeper soil (40-60 cm deep) of the Cassaïre site (future soil surface; grey bars, n=5). Df are the degrees of freedom. The F of ANOVA or the X^2 of Kruskal-Wallis tests are shown above the bars (***: p<0.001, **: p<0.01), bars showing common letters do not have any significant differences according to Tukey post-hoc tests or pairwise multiple comparisons with Bonferroni *p* adjustment.

Organic matter, total C and total N clearly distinguished the soils from the donor sites from those of the Cassaïre along the first axis (73.2%; with an eigenvalue of 5.13 for a total represented of 7) of the PCA (***Figure 3.1.3***). The second axis (18.0%; with an eigenvalue of 1.26 for a total represented of 7) discriminates the deeper Cassaïre soil from surface

Cassaïre soil, and clearly delineates their respective differences in phosphorus and pH (***Figure 3.1.2*** and ***Figure 3.1.3***).

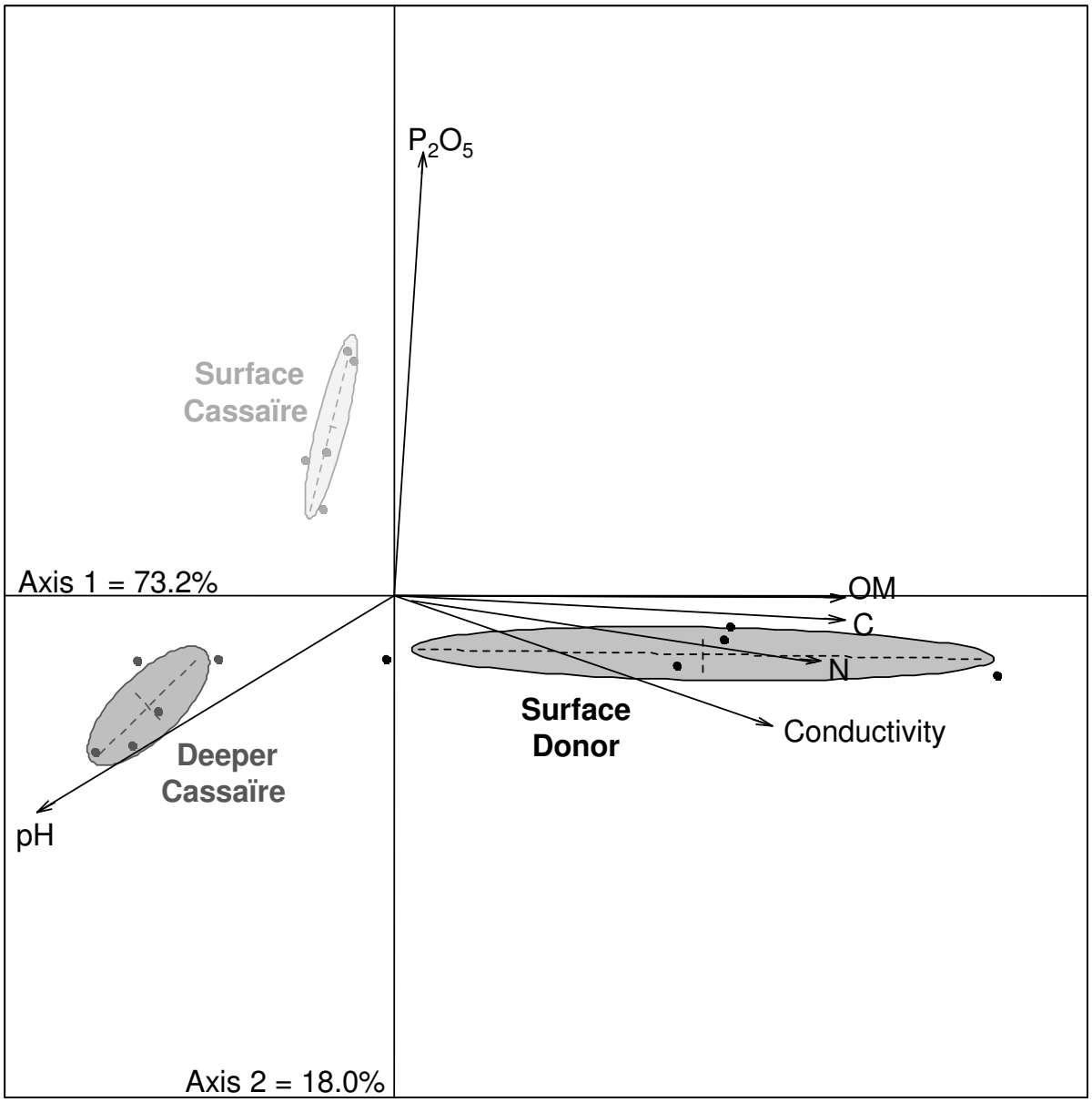

Figure 3.1.3: Ordination plot of the Principal Component Analysis based on soil nutrient contents (15 samples × 6 variables) of surface soil of the donor sites (black, 5 plots), of surface soil of the Cassaïre site (current soil surface; light grey, 5 plots), and of deeper soil (40-60 cm deep) of the Cassaïre site (future soil surface; dark grey, 5 plots). Ellipses are centred on the barycentre and their forms are weighted by the distribution of all points corresponding to the same treatment (surface donor, surface soil, deeper soil).

3.1.3.2. Effect of soil transfer on aquatic vegetation

Plant species richness significantly increased with soil transfer (16.0±2.0) relative to the control (6.3±2.1) and ended up being comparable to that of the donor sites (14.0±2.8)

(*Figure 3.1.4.A*). The aquatic vegetation cover was significantly lower in the control blocks (3.5±2.2%) than in the soil transfer blocks (96.8±4.5%) (*Figure 3.1.4.B*). The aquatic vegetation cover in the latter and at the donor sites (78.8±16.4) was not significantly different (*Figure 3.1.4.B*). The Bray-Curtis similarity index was significantly higher in the soil transfer blocks than in the control and approached the values of the donor sites (*Figure 3.1.4.C*).

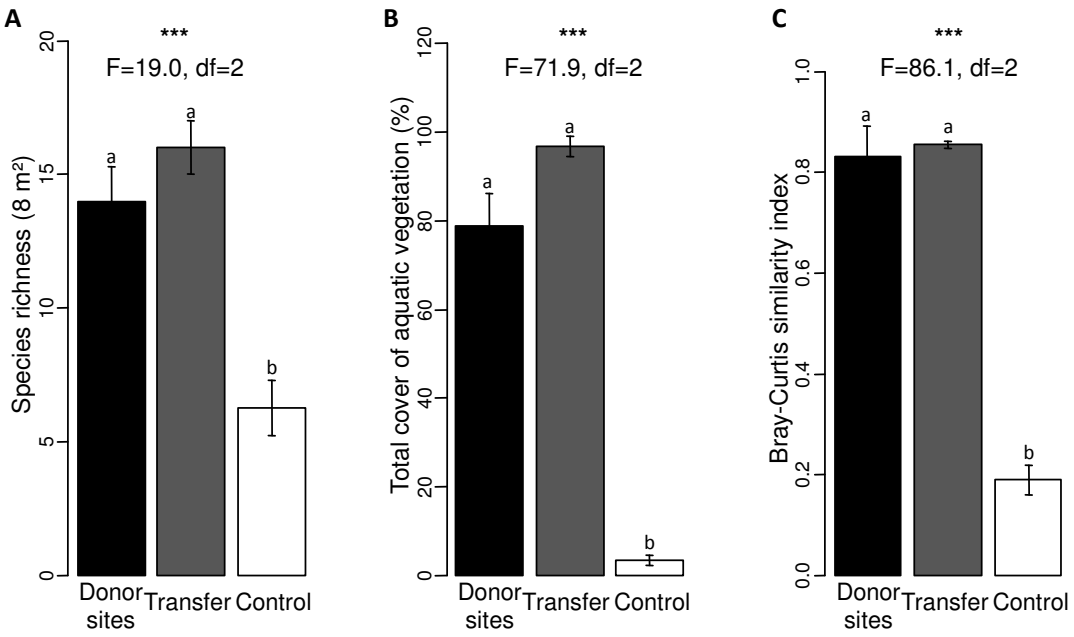

Figure 3.1.4: Mean and standard errors of species richness (8 m²) (A), total cover of aquatic vegetation (%) (B) and Bray-Curtis similarity index on aquatic vegetation (C) between donor sites and i) donor sites (black bars, n=5 plots), ii) soil transfer blocks (grey bars, n=4 plots) and iii) control blocks (white bars, n=4 plots). Df are the degrees of freedom. The F of ANOVA performed are shown above the bars (***: p<0.001), bars showing common letters do not have any significant differences according to Tukey post hoc tests.

The first axis of the CA (41.2%; with an eigenvalue of 0.61 for a total represented of 1.48) discriminated the control blocks from the two other communities: donor sites and soil transfer blocks (*Figure 3.1.5*); control blocks were composed of *Rumex crispus, Poa trivialis* and the exotic species *Lindernia dubia*. The species composition of the transfer blocks was very similar to that of the donor sites that were characterized by target hydrophyte species, such as *Chara aspera*, *Ranunculus peltatus* and *Tolypella glomerata*. These results were confirmed by the nonparametric MANOVA, showing that the soil

transfer treatment did significantly affect plant community composition between control and transfer blocks (dF=1, F= 11.98, *p*=0.024).

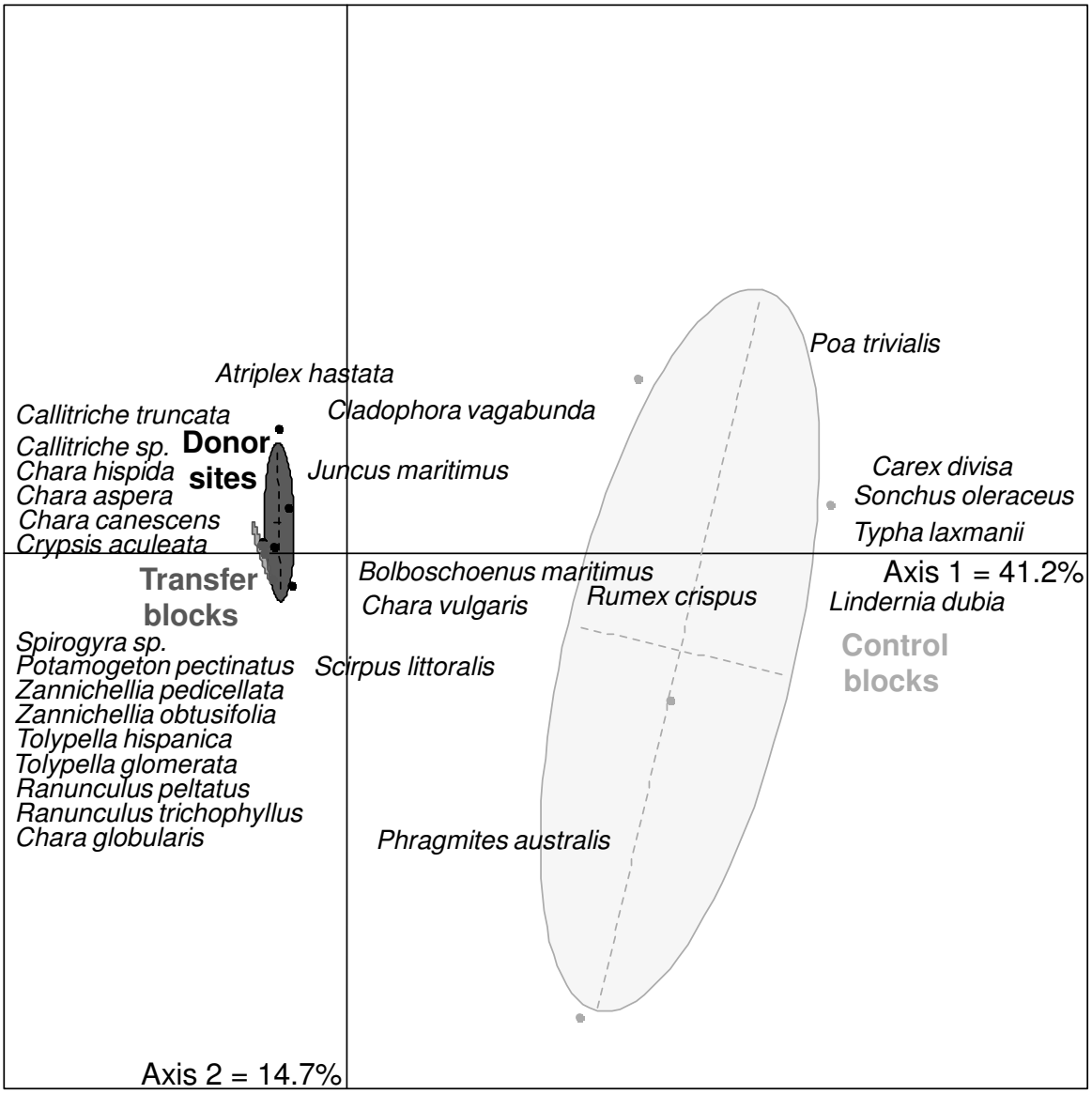

Figure 3.1.5: Ordination plot of the Correspondence Analysis of species abundances (13 plots × 28 species) on donor sites (dark, 5 plots), transfer blocks (dark grey, 4 plots) and control blocks (light grey, 4 plots). Ellipses are centred on the barycentre and their forms are weighted by the distribution of all points corresponding to the same treatment (donor sites, transfer blocks, control blocks).

3.1.3.3. Effect of soil transfer on the different species categories

Active restoration significantly increased the number of target species recorded in the first months after the flooding: compared with the donor sites, the transfer blocks had a significantly higher number of the target species (9.8±1.0 versus 7.8±1.3), which

were totally absent from the control blocks (***Figure 3.1.6.A***). Ricefield hydrophyte weeds were present in all control blocks but absent from the transfer blocks and from the donor sites (***Figure 3.1.6.B***). We found significantly more filamentous algae in the soil transfer blocks than in the control blocks and at the donor sites (***Figure 3.1.6.C***).

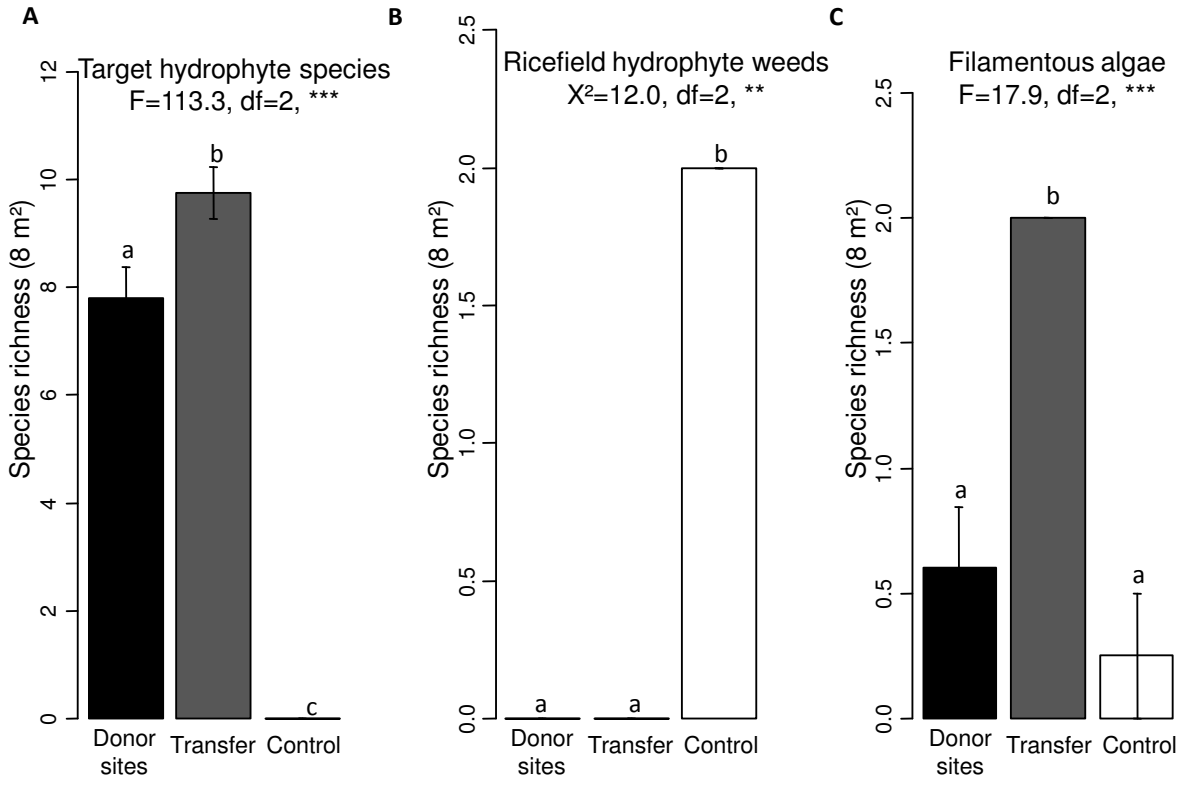

Figure 3.1.6: Mean and standard errors in species number of the different species categories in 8 m² plots: the target hydrophyte species (A), the ricefield hydrophyte weeds (B) and the filamentous algae (C) for donor sites (black bars, n=5 plots), soil transfer blocks (grey bars, n=4 plots) and control blocks (white bars, n=4 plots). Df are the degrees of freedom. The F of ANOVA or the X^2 of Kruskal-Wallis test performed are shown above the bars (***: p<0.001, **: p<0.01), bars showing common letters do not have any significant differences according to Tukey post-hoc tests or pairwise multiple comparisons with Bonferroni *p* adjustment.

3.1.4. Discussion

3.1.4.1. Soil properties

Abiotic conditions can adversely affect the success of plant community transfer, particularly when they are very different from those of the donor ecosystem (Bullock 1998; Dawe et al. 2000). In coastal wetlands, such as the Camargue area, plant communities are mainly driven by the hydroperiod, water depth, and salinity (Grillas 1990)

but soil nutrient conditions also play an important role by directly affecting plant growth (Zedler 2000b). Obtaining soil characteristics close to those of the reference ecosystem is a major objective in restoration projects (Zedler 2000b), in order to establish suitable conditions for target species recolonization (Marrs 2002). In our study, the nutrient concentrations considered were higher at donor sites except for phosphorus, which was higher at the site to be restored. The fertilizer use during cultivation may explain the results because the restoration period following abandonment was quite short for depletion of fertilizer residues. Indeed, organic matter and nutrient concentrations are often higher in the reference wetlands (Galatowitsch and Valk 1996; Zedler 2000b), except for phosphorus, which is strongly related to previous fertilizer use. On one hand soil transfer appears to be a good way to increase organic matter and nutrients concentrations, on the other hand it may also favor the establishment of filamentous algae (Burkholder 2009), that we found more abundantly in the transfer blocks than in the control. The higher pH in the deeper soil that became the surface soil of the blocks did not seem to affect the plant germination probably because it still remained within the pH range appropriate for basophilous plants (i.e. 7.5 to 9; (Wilde 1954).

Upper soil layers of former agricultural lands contain high levels of nutrient favoring most of the ruderal species of the seed bank, and increasing competition (Marrs 2002). The topsoil removal to construct blocks (which will also be removed at the scale of the site to restore the wetland) reduced significantly the content of phosphorus, organic matter, total C and total N, and also to the reduction of unwanted plant species by reducing the seed bank (***Chapter 2***). However, the role of nutrients is probably time limited. If for terrestrial oligotrophic community restoration, soil conditions play an important role for success (***Chapter 4***), requiring nutrient poor site conditions because non-target species from the seed bank can "hijack" the succession, in wetland ecosystem, hydrology seems to play a determining role on plant communities which can buffer the effects of soil conditions, by eliminating species that are not adapted to summer drought or to winter flooding. However high nutrient levels may lead to a spread of filamentous algae, that may prevent the installation of temporary wetland communities (Hosper 1998).

3.1.4.2. Natural colonization

Many of the naturally colonizing species which established in the control blocks in the five first months were abundant in the seed bank of the area (seed bank sampling using the seedling emergence with sample concentration method, **Chapter 2**). *Rumex crispus, Poa trivialis,* and *Sonchus oleraceus*, as well as the aquatic species *Lindernia dubia* and *Chara vulgaris*, were the main species found in the control blocks. *Lindernia dubia,* a common exotic species of ricefields and *Chara vulgaris*, a cosmopolitan algae had been favored by water management during rice cultivation (i.e. summer inundation), are typical ricefield weeds occurring in seed bank (Marnotte et al. 2006) and reflecting land use history of the area. Nevertheless, their abundance will decrease as summer drought does often not allow to finish their life cycle (they flower in early summer). Ruderal and meadow species should also rapidly disappear after several flooding periods. The Mediterranean hydrology should play a major role as a filter to eliminate species that are not adapted to summer drought (ricefield weeds) or to winter flooding (ruderals and terrestrials species).

Five months after the creation of the blocks, most plant species established from the seed bank of the control blocks. Aquatic plants may establish from the seed bank (Leck 2003; De Steven et al. 2006) but also by seed deposition through water dispersal (Mitsch et al. 1998), waterbirds (Figuerola et al. 2002; Figuerola and Green 2002b; Brochet et al. 2010b), vertebrates (Zedler and Black 1992), or wind dispersal (Reinartz and Warne 1993). However, these mechanisms of colonization are not efficient, because dispersal is slow and sometimes unlikely (Moreno-Mateos and Comin 2010). In our study, no target species were found in the control blocks. The time span is too short to evaluate the potential of natural colonization from the external seed pool. Although rice cultivation dominates the surrounding landscape, natural temporary wetlands still occur within distance of less than 1 km and dispersal by waterbirds, a major dispersal vector (Brochet et al. 2010b), seems to be possible. However, the size of our blocks may have been too small to be attractive for waterbirds. This weak attractiveness will be overcome when the 35 hectare wetland will be restored, as it will be more attractive for waterbirds (Pirot et al. 1984); zoochorous processes will then be playing their role in the dispersion of aquatic species.

Spontaneous succession alone has been shown to allow the restoration of plant communities and active restoration is not necessary if target species occur at the site or if sites are connected to propagule sources (Dawe et al. 2000). However, sites situated in agricultural landscapes or with a long history of cultivation, such as the Cassaïre area, often show a weak ability to restore passively due to the lack of target species in the seed banks and/or few target seed sources (Galatowitsch and Valk 1996; De Steven et al. 2006; Collinge and Ray 2009). Moreover, on abandoned croplands, ruderal species may predominate, slowing down succession and preventing the establishment of target species (Prach et al. 2001a). In such cases, soil transfer may be an efficient method to accelerate succession.

3.1.4.3. Effect of soil transfer on the aquatic plant community

Soil transfer increased the total species richness and allowed the establishment of all the aquatic target species. The plant composition of the transfer blocks was close to that of the donor sites. The differences in soil nutrients between the donor sites and the transfer blocks did not prevent germination of the aquatic species that were transferred with the soil in the blocks.

In grassland ecosystems, Jaunatre *et al.* (2012) showed an increase in the non-target species after soil transfer compared with the reference grassland, resulting from soil disturbance induced by the transfer itself. Bullock (1998), also working in grassland ecosystems restoration, showed that the transfer led to communities with species that are very different from those of target communities. Highly selective stress conditions leading to very predictable successional trajectories (Mesléard et al. 1999) may explain the observed general success of soil transfer in wetlands as well as the promising results of the present study in contrast to the observed response of terrestrial communities in which selection is less strong. In aquatic ecosystems, the selection of plant communities by the water filter is important, only aquatic species can survive in the environment. This filter has an important selective effect, especially in our case, where the water regime is temporary, increasing selection pressure (the species should be aquatic and tolerated stages of drought, i.e. be annual). For terrestrial communities, even though there may be obvious stressful conditions (e.g. drought), restoration is often done following

agricultural abandonment on land (***chapter 4***) with a nutrient-enriched soil and a seed bank dominated by ruderal species, both favoring seed bank species and competition with target species (***chapter 4***).

3.1.4.4. Other benefits of soil transfer

In addition to target species introduction, soil transfer seems to significantly reduce the establishment of undesired species emerging from the seed bank and from the surroundings, such as ricefield weeds. The increase in the cover of aquatic vegetation seems to prevent the germination and growth of these weeds. The initial species composition of the restored vegetation potentially affects the vegetation for a long time (Vécrin et al. 2002) and non-desirable species installed at the beginning can persist, hampering succession and/or changing the vegetation trajectory (Prach et al. 2001a; Prach and Pysek 2001; Prach et al. 2001b; De Steven et al. 2006). Soil transfer may also reduce stochasticity, by immediately installing a stable community (Weiher and Keddy 1995). Collinge and Ray (2009) and Reinartz and Warne (1993) have shown that wetlands that initially received more native seeds were less prone to colonization by exotic species, and that the early introduction of native wetland species may increase the long-term diversity of communities in created wetlands. Indeed, in our case, the ricefield weeds can compete with our target hydrophyte species. Although they are less adapted to the temporary wetland and tend to disappear over time, a certain plasticity of their phenology allowed their presence in the blocks and can thus compromise succession and prevent the natural reestablishment of target species. Soil transfer appears to be an appropriate method to accelerate succession towards the desired plant community and to attempt to bypass some of blocked stages of succession (Reinartz and Warne 1993; McKinstry and Anderson 2005; Collinge and Ray 2009).

Soil transfer provides an advantage for rare species showing dispersal limitation. Indeed, some studies have shown that passive methods may not allow the full restoration of the reference species composition (De Steven et al. 2006; Collinge and Ray 2009).

In using soil transferred from several donor sites, we increase the number of target hydrophyte species at one site compared with a single donor site. We further increase the pool of available species, allowing the selection of the most appropriate species to the

specific abiotic conditions of the Cassaïre site, and thereby increasing the probability of success (Zedler 2000b). Soil transfer also provides a soil seed bank ensuring survival in fluctuating environments. This dormant reservoir is a powerful mechanism for maintaining species diversity by promoting the coexistence of a greater number of species.

In addition, soil transfer allows i) the preservation of biotic interactions by transferring soil microorganisms (Bullock 1998) which play an important role in structuring plant community (Moora and Zobel 2009) and in improving substrate conditions (McKinstry and Anderson 2005) and ii) the potential transfer of zooplankton and macroinvertebrate egg bank (***Chapter 3.2***). Brady and coauthors (Brady et al. 2002) demonstrated that soil transfer leads to a more natural invertebrate community structure, and can be a significant benefit for non-aerial invertebrates, which are not able to disperse alone, such as crustaceans (*Cladocera* and *Triops*) or mollusks.

3.1.4.5. Restoration perspectives and the importance of time and monitoring

The positive results obtained in the blocks after only few months and the low technical effort demonstrate that soil transfer is a promising restoration method that may also be applied at larger scales (i.e. creating 35 hectares of Mediterranean temporary wetlands in our site). Indeed, unlike terrestrial ecosystems where soil transfer involves the destruction of the donor ecosystem (Vécrin and Muller 2003; Jaunatre et al. 2012) and cannot be a substitute for *in situ* conservation (McLean 2003), the soil transfer technique used in our study appears a non-destructive method at the scale of the donor wetlands. Because the seed bank of the first few centimeters of the soil in temporary wetlands is rich in seed number and species diversity (Bonis and Grillas 2002), only 8 m^2 of soil were collected in our case at the donor sites (corresponding approximately to less 0.001% of the total area of the donor sites) and were spread for half a day over 32 m^2 (corresponding to 200 liters of soil) in the blocks. The low quantities of soil required allow an application of the method at a scale of several hectares. Moreover, instead of spreading the soil over the whole area, soil may be transferred in small patches, functioning as species-rich sources for spontaneous colonization of nearby areas not transferred.

Short-term observations are not sufficient in predicting community dynamics (Mesléard et al. 1991; Weiher et al. 1996; Collinge and Ray 2009). An initial success may be compromised by long-term mortality, undesired successional trajectories, and does not reflect long-term success (Dawe et al. 2000; Fahselt 2007), although long-term studies confirm a beneficial role of soil transfer in wetland restoration (Reinartz and Warne 1993; Balcombe et al. 2005a; Nishihiro et al. 2006). Long-term monitoring of changes in plant community of restored wetlands is required to evaluate the potential of this technique for restoring or creating Mediterranean temporary wetlands.

Section 3.2: Effectiveness of soil transfer in restoring Mediterranean temporary wetland invertebrate communities

Muller Isabelle, Aline Waterkeyn, Elise Buisson, François Mesléard & Hector Rodriguez

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3.2.1. Introduction

Because zooplankton and macroinvertebrates play important roles in wetland ecosystems, such as influencing sediment properties and water content (Rhoads and Young 1970), they are extremely valuable components of wetland ecosystem functioning. In spite of this, ecological restoration has been more focused on abiotic and plant components, with limited attention given to the fauna in general and the invertebrates in particular (e.g. Palmer *et al.* 1997; Keesing and Wratten 1998; Zedler 2000b; Longcore 2003; Cristescu *et al.* 2013). It is often assumed that animals will naturally recolonize a site when the native plant community and suitable habitat conditions are present (Palmer et al. 1997; Keesing and Wratten 1998), although this paradigm has recently been questioned and tested (Block et al. 2001; Brady et al. 2002; Koch 2007; Cristescu et al. 2013).

Several studies of natural colonization processes in restored wetlands show that some invertebrate taxa found at natural sites are able to colonize sites after the restoration of habitat conditions (LaSalle et al. 1991; Brown et al. 1997; Balcombe et al. 2005b; Obolewski and Glińska-Lewczuk 2011). The proximity of natural wetlands is then a determining factor for reducing dispersal limitations and for favoring the development of faunal communities (Paterson and Fernando 1969; Sacco et al. 1994; Levin et al. 1996; Chovanec and Raab 1997; Badosa et al. 2010). However, as Zedler (2000a) pointed out, "it takes more than water to restore a wetland": the assumption that providing the correct habitat structure will naturally lead to the recovery of the appropriate communities (Palmer et al. 1997) is rarely demonstrated. Indeed, with natural recruitment, e.g. passive restoration, dispersal-limited species are less likely to appear (Zedler 2000a; Louette et al. 2009) and the recovery of the community may be limited by the capacity of some organisms to be recruited (Bradshaw 1996; Palmer et al. 1996), which adversely affects the success of restoration. Most aquatic insects, such as dragonflies (Odonata), water bugs (Hemiptera), water beetles (Coleoptera), flies and mosquitos (Diptera), are good dispersers because they are, at least for part of their life cycles, capable of active flight. Most of them can therefore select their habitat (Heck and Crowder 1991; Palmer et al. 1996; Zedler 2000b). However, other macroinvertebrates, such as Gastropoda, Amphipoda and Isopoda, and zooplankton species, such as Rotifera, Cladocera,

Copepoda, Ostracoda, Anostraca, Notostraca and Spinicaudata, are dependent on external vectors for their, less efficient, passive dispersal (Barnes 1983; Sacco et al. 1994; Brown et al. 1997; Jenkins and Underwood 1998). This could lead to major differences in community structure between restored and natural wetlands which are dominated by highly mobile taxa having aerial dispersal capabilities (Barnes 1983; Layton and Voshell 1991; Levin et al. 1996; Brown et al. 1997), persisting for a long time, and having important consequences for the recovery of wetland ecological processes (Barnes 1983).

In achieving restoration goals, the limited dispersal abilities of certain species of interest can be overcome by active restoration such as stoking (direct introduction of individuals of taxa with low dispersal) or transferring soil containing an egg bank (inoculating soil harvested from a natural wetland) to facilitate the establishment of these taxa (Levin et al. 1996; Keesing and Wratten 1998; Gleason et al. 2004; Chittapun et al. 2005). Active restoration is a common procedure for restoring plant communities in wetland ecosystems (Reinartz and Warne 1993; Kaplan et al. 1998; Nishihiro et al. 2006; ***Chapter 3.1***), but relatively few studies have documented the efficiency of this procedure in restoring macroinvertebrates and zooplankton communities (Brown and Bedford 1997; Brown et al. 1997; Brady et al. 2002; Tong et al. 2013). Brady and coauthors (2002) have demonstrated that inoculating natural wetland soils and stocking weak disperser species can increase invertebrate diversity, non-aerial invertebrates, and result in community structures more similar to those found in natural wetlands. Brown et al. (1997) came to the same conclusion using only inoculation of natural wetland soils, increasing overall macroinvertebrate numbers accompanied by an abundance of some less mobile taxa.

In the Mediterranean Basin, temporary wetlands are probably among the most remarkable, but also the most threatened of wetland habitats (Grillas et al. 2004). These wetlands are characterized by winter and spring flooding, with durations that vary greatly from year to year, and by a complete drying-out in summer (Grillas et al. 2004). They are of high conservation value because they often house unique fauna and flora, contribute significantly to regional diversity, and fulfill an important role in the landscape (Grillas et al. 2004; Zacharias et al. 2007). Therefore, in recent decades, the restoration of temporary wetlands has received increased attention (Zhang et al. 2010).

Many organisms inhabiting these ecosystems exhibit adaptations for surviving the dry phase as dormant eggs or other drought-resistant life stages that persist in wetland sediments (Wiggins et al. 1980; Williams 1998). Inoculating restored sites with wetland sediments collected at natural sites during the dry period can be a useful method of restoring temporary wetlands and increasing their functionality, provided the introduced sediments contain a persistent and viable egg bank (Brown and Bedford 1997; Brady et al. 2002; Tong et al. 2013). This method has been shown to immediately increase plant species richness as well as the number of target hydrophyte species, leading to a vegetation composition close to that of the ecosystem of reference (***Chapter 3.1***). Such soil transfer could also play a role in restoring the invertebrate community by (1) directly facilitating the establishment of populations of poorly dispersing taxa with dormant stages and (2) indirectly attracting actively dispersing taxa with an adapted vegetation and food web. Indeed, developed vegetation stands can promote invertebrate establishment by providing a refuge from predation, and for reproduction, and a source of food (Rozas and Odum 1988; Heck and Crowder 1991; Moy and Levin 1991; Korsu 2004; Tong et al. 2013). On the other hand, high zooplankton prey densities can also support larger macroinvertebrate predator populations (Lynch 1979; Cooper 1983; Rabe and Gibson 1984).

The present study tests the effect of soil transfer from temporary wetlands, which has been successfully used to restore plant communities (***Chapter 3.1***), on invertebrate communities. The objective of this on-site experiment on wetland blocks is to assess how soil transfer can benefit zooplankton and macroinvertebrate communities. We addressed two questions: (1) By introducing soil do we increase zooplankton and macro-invertebrates diversity? (2) Does soil transfer result in invertebrate communities more similar to those of natural wetlands?

3.2.2. Methods

3.2.2.1. Study site

The experiment was conducted on the Cassaïre site (c. 43°31’ N, 4°44’ E, 3 meter maximum elevation), located in the east of the Camargue area (Rhône delta, Southern

France, ***Figure 3.2.1***). The climate is typically Mediterranean, characterized by an annual average temperature of 15°C, an annual rainfall of 550 mm (mainly concentrated in autumn), and a summer drought. The site has been subject to recurrent leveling for rice cultivation since the 1940s, eliminating the natural topography. Cultivation definitively ended in 2004. A restoration project was initiated on this site to recreate a large Mediterranean temporary wetland as typically found in the nearby Camargue area.

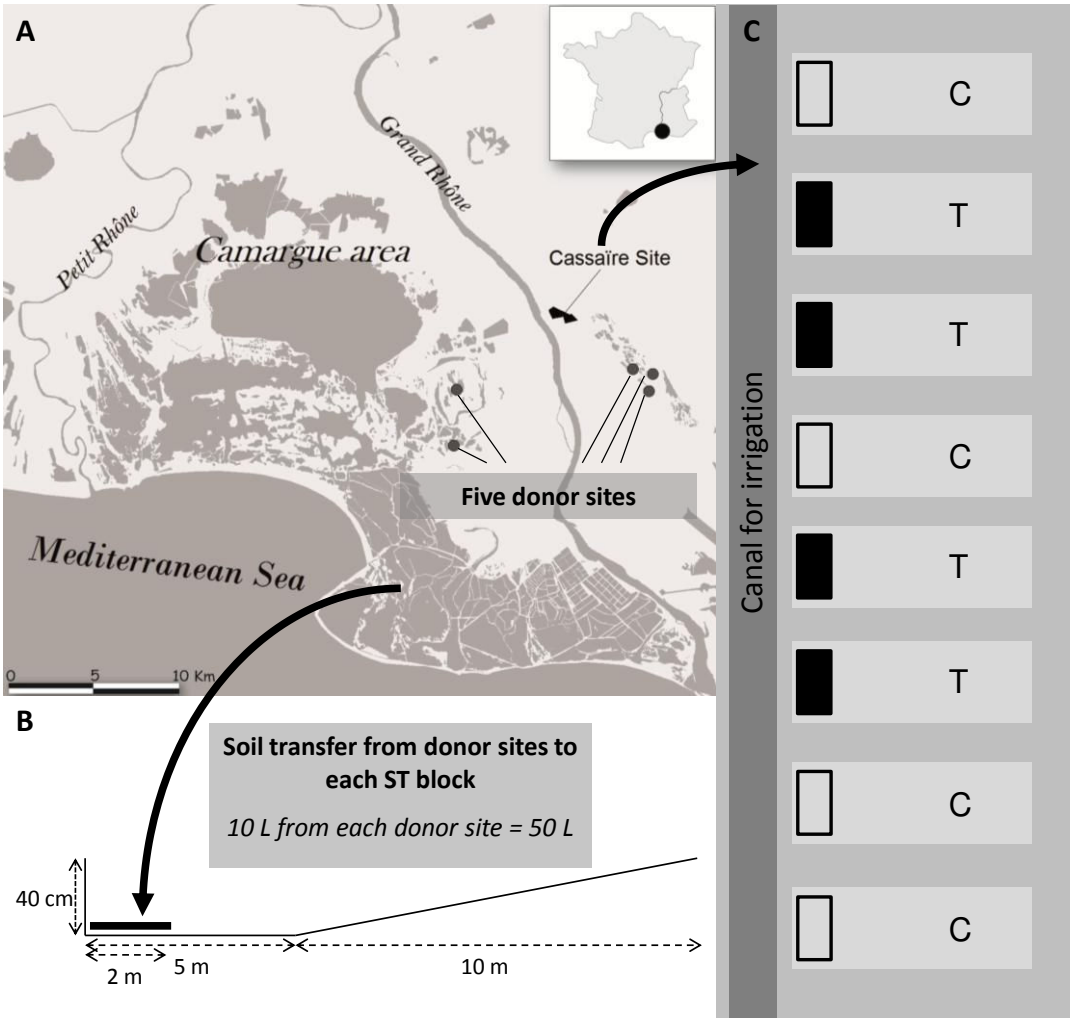

Figure 3.2.1: Locations of the Cassaïre site (in black) and the five donor sites (grey circle). The light grey shading indicates the wetlands of the Camargue area (A). Side view of one soil transfer block (B). Experimental design of restoration treatments at the Cassaïre site (C). C = control blocks and T = transfer blocks (black rectangle indicates the soil transfer).

3.2.2.2. Experimental design and soil transfer

Five natural temporary wetlands in the surrounding area were selected as soil donor sites (distance between 1 and 6 km from the Cassaïre site, ***figure 3.2.1.A***), based on their

aquatic plant communities (***Chapter 3.1***). The environmental conditions in these five donor wetlands varies slightly from one wetland to another, but corresponded to the range of expected environmental conditions on the Cassaïre site after the creation of the temporary wetland, i.e. having a flooding period from September to June, a maximum water depth of 30 cm, and salinity below 6g/L. Not every target hydrophyte plant species could be found in a single donor wetland; rather, the five donor sites together provide a regional, locally adapted target species pool. In August 2011, during the dry period, we collected eight 45 × 45 cm sediment samples from a 3 cm depth corresponding approximately to a total of 40 L per donor site. Our assumption was that these collected soils would contain the seeds and eggs of the species present in the donor sites. We pooled the 8 samples together and blended them using a cement mixer. The resulting single bulk sample was stored dry until the transfer to the Cassaïre site.

To simulate the suitable environmental conditions characteristic of a Mediterranean temporary wetland, eight blocks with a gentle slope were dug out (15 m long × 5 m large × 40 cm deep; ***Figure 3.2.1.B***) along an irrigation canal. Four blocks were used to test soil transfer (transfer blocks). The four other blocks (control blocks) were used to monitor natural colonization and establishment. The position of treatments was randomized (***Figure 3.2.1.C***). We pooled 10 L samples from each of the five sites and we spread the 50 total L of soil on a 4 × 2 m plot at the bottom of each transfer block (***Figure 3.2.1.B***). A pump was used to maintain a constant 20 cm water level for a time period beginning the day after the transfer in January and ending in late June 2012. This is intended to reproduce the flooded conditions associated with temporary wetland.

3.2.2.3. Zooplankton and macroinvertebrates sampling

In mid-June 2012, 5 months after applying treatments, zooplankton and macroinvertebrate sampling were conducted. This was followed by measurements of dissolved oxygen ($mg.L^{-1}$), conductivity ($mS.cm^{-1}$), and temperature (°C) in each block. We observed no significant differences in chemical parameters between transfer blocks and control blocks (***Figure 3.2.2***).

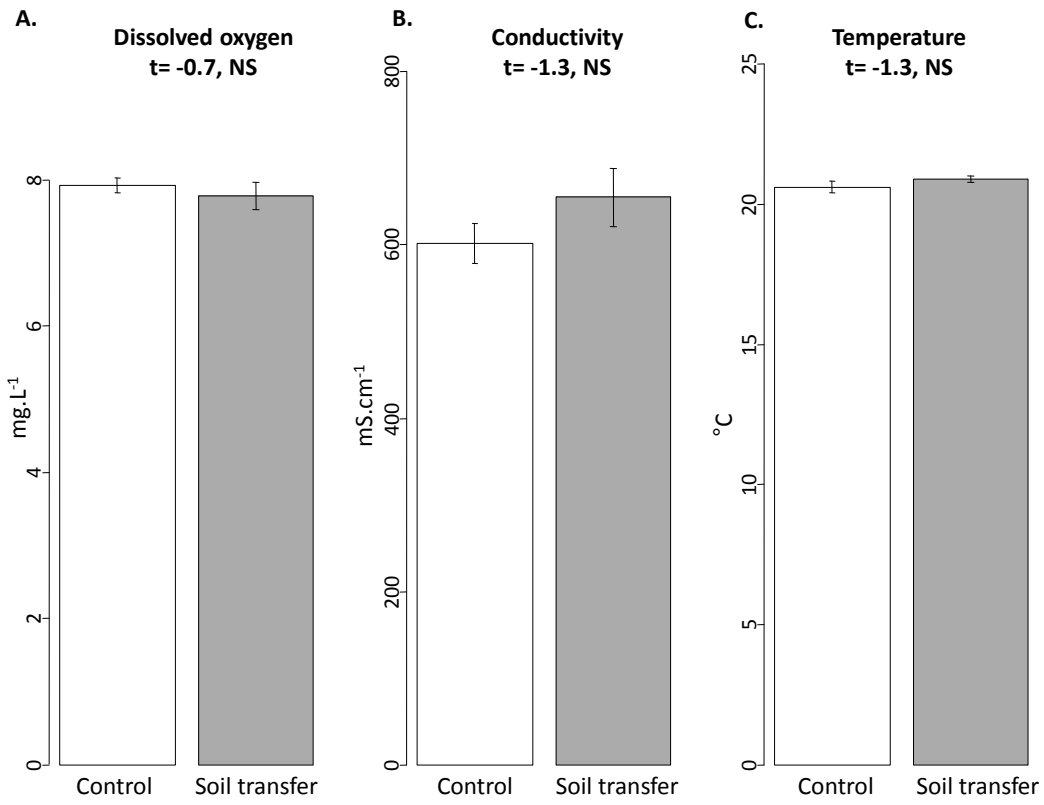

Figure 3.2.2: Mean and standard errors of dissolved oxygen (A), conductivity (B), and temperature (C) in control blocks (white, n=4) and in soil transfer blocks (grey bars, n=4). The t of Student test performed are shown above the bars (NS: non significant).

For zooplankton, we collected 50 L of water at different depths in each block and filtered the collected water though a 64 µm mesh. Macroinvertebrates were sampled by performing a 1-minute sweep of a 250 µm net through all of the microhabitats (the water column and the vegetation). The zooplankton and macroinvertebrates were stored in ethanol (70%), counted, and identified under a binocular dissecting microscope. Zooplanktons were identified to class level and macroinvetrebrates were identified to class, family, or genus level. We classified all taxa found in non-aerial and in aerial taxa. When the taxa were observed in a larval stage, it was noted. Taxonomic levels were not identical between taxa, but for each taxon the level of taxonomic identification was identical between blocks.

Thirty natural temporary wetlands (comprising two of the five donor sites), selected along a broad salinity and hydroperiod gradient, were also sampled. The zooplankton and macro-invertebrate communities were sampled using the same method and the same level of identification (Waterkeyn et al. 2008) as was done for the study blocks.

In order to determine whether soil transfer can modify the functional composition in terms of feeding behavior (Moog 1995), we attributed each taxon to one or several functional-feeding guilds (Moog 1995):

- Shredders (SHR): Fallen leaves, plant tissue, coarse particulate organic matter
- Grazers (GRA): Epilithic algal tissues, biofilm, partially particulate organic matter
- Active filter-feeders (AFIL): Food in water current (suspended fine particulate organic matter, coarse particulate organic matter and prey) is actively filtered
- Passive filter-feeders (PFIL): Food (suspended fine particulate organic matter, coarse particulate organic matter and prey) brought by flowing water current
- Detritus feeders (DET): Sedimented fine particulate organic matter
- Miners (MIN): Leaves of aquatic plants
- Xylophagous (XYL): Woody debris
- Predators (PRE): Prey
- Omnivorous animals (OTH): Diverse

Because the diets of some organisms are not exclusive, each taxon was given a score out of 10, broken down by functional feeding guild in such a was as to represent the relative contributions of each of the 9 guilds to the taxon's overall nutrition (Moog 1995): e.g., for Chironomini: SHR=0, GRA=0, AFIL=3, PFIL=0, DET=7, MIN=0, XYL=0, PRE=0, OTH=0, total score/taxon=10.

To determine the composition of functional feeding guilds in each block, the number of individuals of each taxon was first weighted by the functional feeding guild scores (e.g. for 92 Chironomini in block#1: SHR=0×92, GRA=0×92, AFIL=3×92, PFIL=0×92, DET=7×92, MIN=0×92, XYL=0×92, PRE=0×92, OTH=0×92). We then summed the weighted scores of all taxa in each functional feeding guild, and then divided by the sum of the weighted scores across guilds, resulting in a frequency of each guild in each block.

3.2.2.4. Data analysis

3.2.2.4.1. Effect of soil transfer on community composition

In order to study the effect of treatment (soil transfer/control) on the community compositions of zooplankton and macroinvertebrates, we used a nonparametric

multivariate analysis of variance (nonparametric MANOVA) (Anderson 2001). We used Bray-Curtis dissimilarities on abundances with 999 permutations to calculate *p*-values. We run separate analyses for zooplankton and for macroinvertebrates data. We also ran a Correspondence Analysis (CA; Greenacre 1984) on both macroinvertebrate and zooplankton compositions.

Diversity was assessed using the number of taxa, the Shannon index, and the Shannon evenness (Pielou 1969), in zooplankton communities and in macroinvertebrate communities. Statistical differences between treatments were measured with Student tests. We also tested differences between treatments in total zooplankton abundance, total macroinvertebrate abundance, among functional feeding guilds and among richness of aerial and non aerial taxa, relative abundance of non aerial taxa and relative abundance of larval stages with Student tests, when parametric assumption were reached, or with Wilcoxon tests, when data were not normally distributed. We performed for each taxa a student test on abundances (when abundances were not normally distributed, data were log (w+1) transformed before testing) to identify differences in abundance between treatments.

3.2.2.4.2. Comparison with natural temporary wetlands

In order to characterize the effect of soil transfer on the invertebrate community, we calculated community similarity with the Jaccard similarity index (Jaccard 1901) between each block and natural wetland composition, resulting in four replicate Jaccard indexes for each treatment. An index of zero corresponds to an absence of species in common between the treatment and the reference community, while an index of 1 indicates a similar invertebrate composition. These four replicate indexes were compared among treatments using student tests.

All tests were performed using R 2.12.0 (R Development Core Team, 2010) with a *p*=0.05 threshold using "ade4" package (Chessel *et al.*, 2004; Dray and Dufour, 2007; Dray *et al.*, 2007) and "vegan" package (Oksanen *et al.*, 2008).

3.2.3. Results

3.2.3.1. Effect of soil transfer on zooplankton community composition

After five months, three taxa, representing 4417 individuals, were identified in both treatments. The soil transfer treatment significantly affected the zooplankton community composition (df=1; F=4.8, *p*=0.028), although the CA (***Figure 3.2.3***) did not clearly discriminate the two treatments because all the three taxa were found in both treatments.

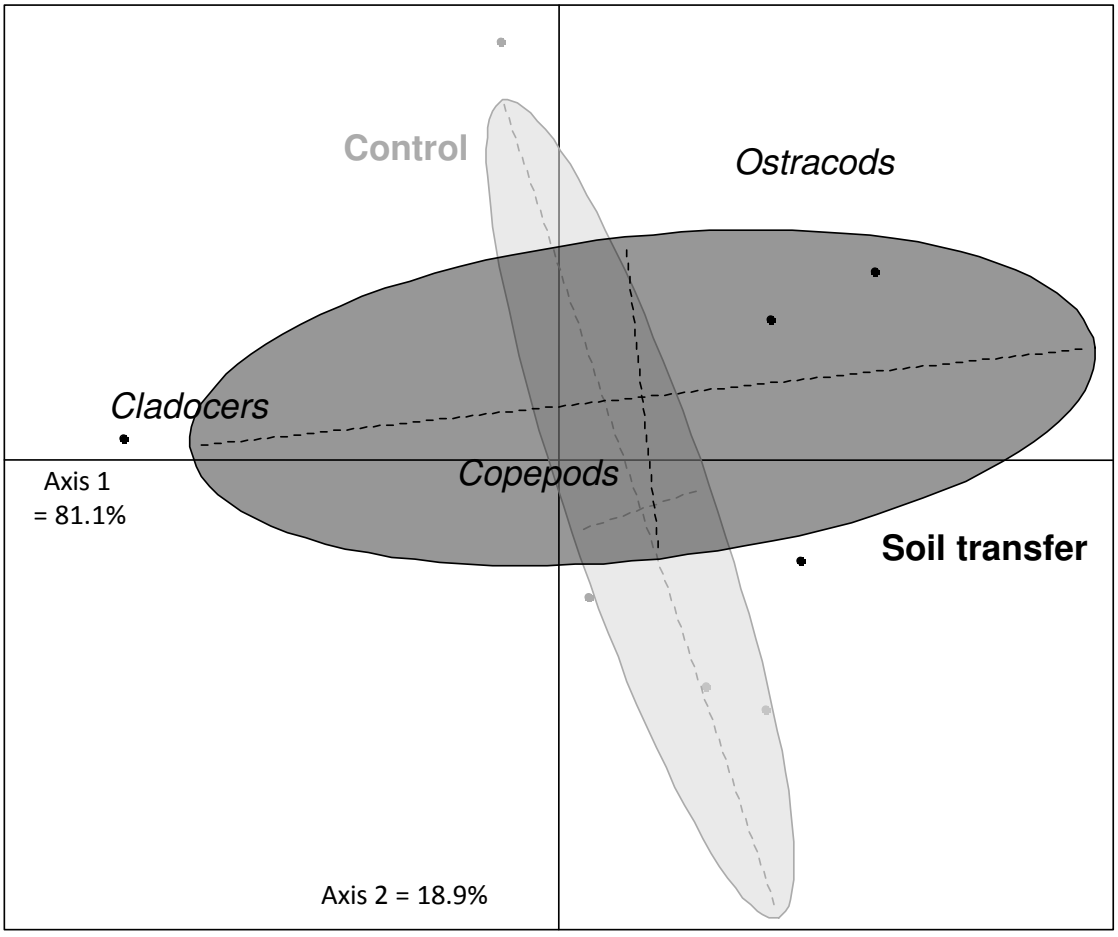

Figure 3.2.3: Ordination plot of the Correspondence analysis based on the zooplankton composition in soil transfer blocks (dark grey, n=4) and in control blocks (light grey, n=4). Ellipses are centered on the barycenter and their forms are weighted by distribution of all points corresponding to the same treatment.

Zooplankton abundance was significantly higher in the soil transfer blocks (828.8±180.3 zooplankton individuals in soil transfer blocks *vs.* 275.5±96.0 individuals in the control block; ***Figure 3.2.4.A***).

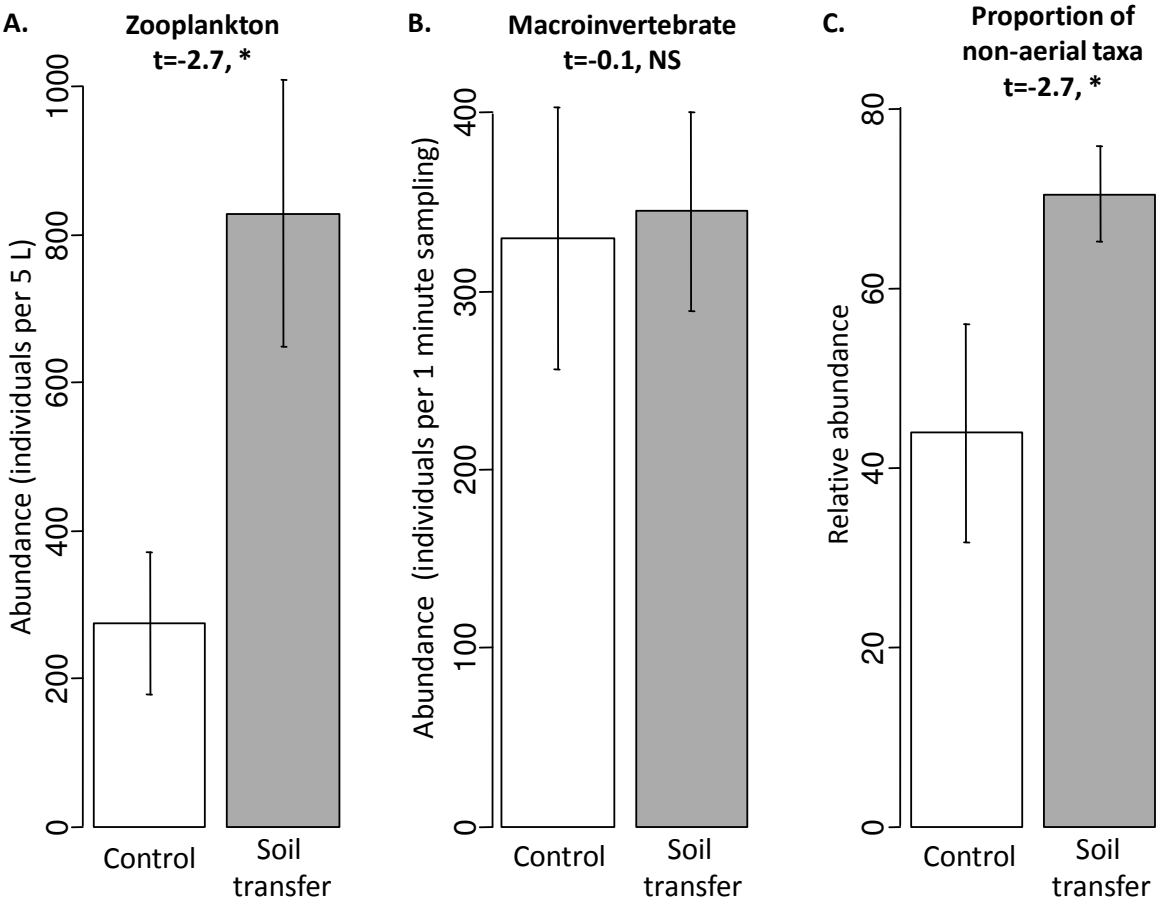

Figure 3.2.4: Mean and standard errors of total zooplankton abundance (A) total macroinvertebrate abundance (B) and proportional abundance of non-aerial taxa (C) in control blocks (white, n=4) and soil transfer blocks (grey bars, n=4). The t of Student test performed are shown above the bars (NS: non significant, *****: p<0.05).

This can be attributed to the significantly higher abundance of copepods (799.5±164.5 copepods individuals for soil transfer *vs.* 271.5±95.0 copepods individuals for control; ***Figure 3.2.5.A***) and ostracods (7.6±2.5 ostracods individuals for soil transfer *vs.* 0.8±0.5 ostracods individuals for control; ***Figure 3.2.5.B***) in soil transfer blocks. No significant difference in species richness, Shannon index, or Shannon evenness between treatments (t=-1.6, *p*=0.21; t=-0.5, *p*=0.65; t=0.4, *p*=0.95 respectively) was observed.

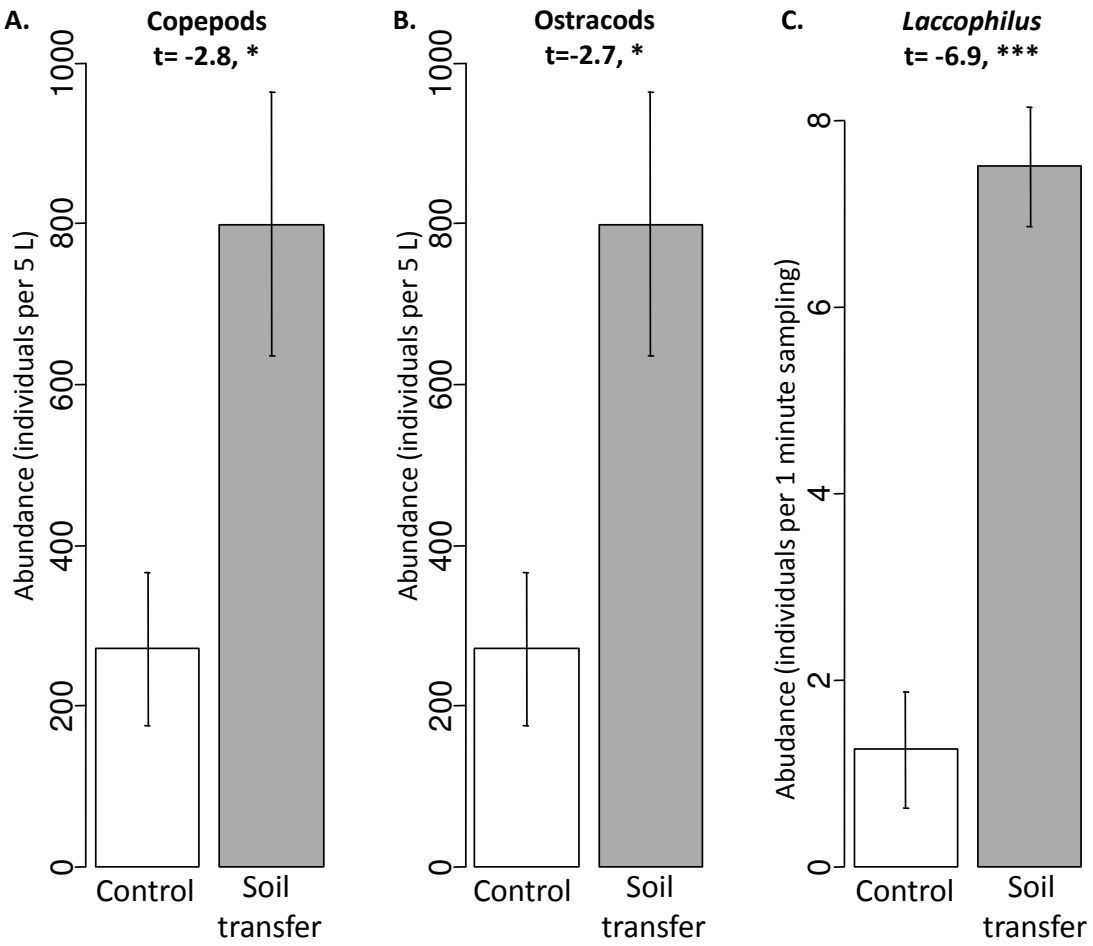

Figure 3.2.5: Mean and standard errors of abundance of copepods (A), ostracods (B) and *Lacophilus* (C) in control blocks (white, n=4) and soil transfer blocks (grey bars, n=4). The t of Student test performed are shown above the bars (*: $p<0.05$, ***: $p<0.001$).

3.2.3.2. Effect of soil transfer on macroinvertebrates community composition

Concerning macroinvertebrates, 39 taxa were recorded in the blocks, representing a total of 2558 individuals. Ten taxa were exclusively found in the soil transfer blocks, including seven coleoptera, two odonata, and one gasteropoda. Five were entirely absent from the soil transfer blocks, one coleopteran, one odonata, one heteroptera, and two diptera. However, a nonparametric MANOVA did not detect any effect of treatment on the macroinvertebrate community composition (df=1, F=0.74, p=0.55). This is confirmed by the CA (***Figure 3.2.6***), which does not clearly discriminated between the two treatments and where the projection of the two communities overlaps.

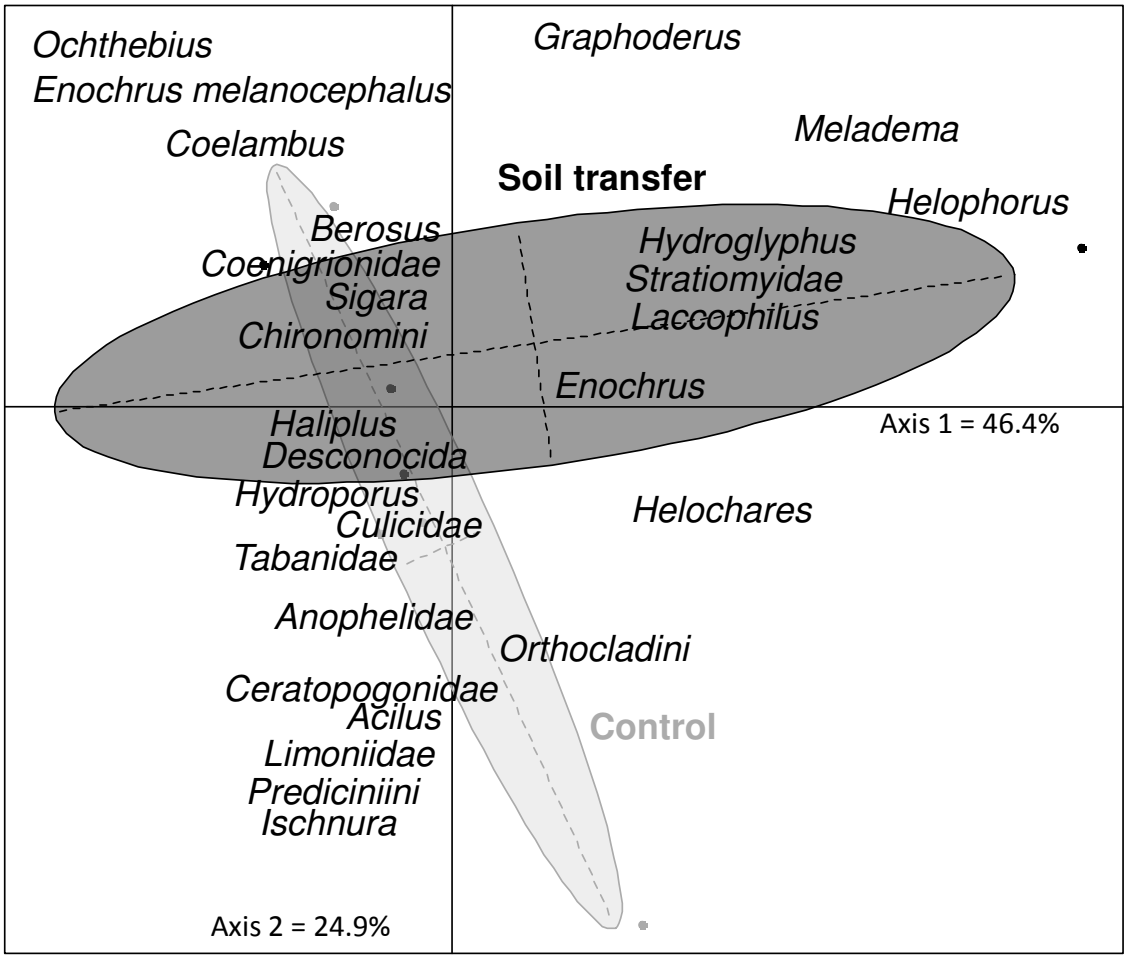

Figure 3.2.6: Ordination plot of the correspondence analysis based on the macroinvertebrate composition in soil transfer blocks (filled circles, grey, n=4) and in control blocks (open circles, white, n=4). Ellipses are centered on the barycenter and their forms are weighted by the distribution of all points corresponding to the same treatment. In the interest of clarity, only the 27 taxa with the higher contributions to axes are shown.

Of the 39 taxa, only *Lacophilus* abundances (coleoptera), were significantly different between the two treatments (2.5±1.3 *Lacophilus* individuals in the control blocks *vs.* 6.3±1.8 *Lacophilus* individuals in the soil transfer blocks; t=-6.9, $p<0.001$; ***Figure 3.2.5.C.)***. Although species richness, Shannon index, Shannon evenness, and abundance of macroinvertebrates (***Figure 3.2.4.B***) were higher in the soil transfer blocks, no significant difference was recorded between treatments for these four parameters (t=-1.2, $p=0.32$; t=-1.7, $p=0.16$; t=-1.7, $p=0.15$; t=-0.2, $p=0.88$ respectively).

While there was no observed difference in the number of aerial and non-aerial taxa between the two treatments (t=-0.9, $p=0.4$ for aerial, and t=-1.6, $p=0.22$ for non-aerial), the relative abundance of invertebrates without aerial dispersal (all zooplankton and the

gasteropoda *Planorbis*) was significantly higher in the soil transfer blocks (71±3% for soil transfer *vs.* 44±12% for control; ***Figure 3.2.4.C***),

The macroinvertebrate communities showed no significant difference when compared based on the six functional feeding guilds (no Omnivorous animals, Xylophagous and Passive filter-feeders were recorded, ***Figure 3.2.7***) or of developmental stages (t=2.1, *p*=0.09 for the relative abundance of larval stages).

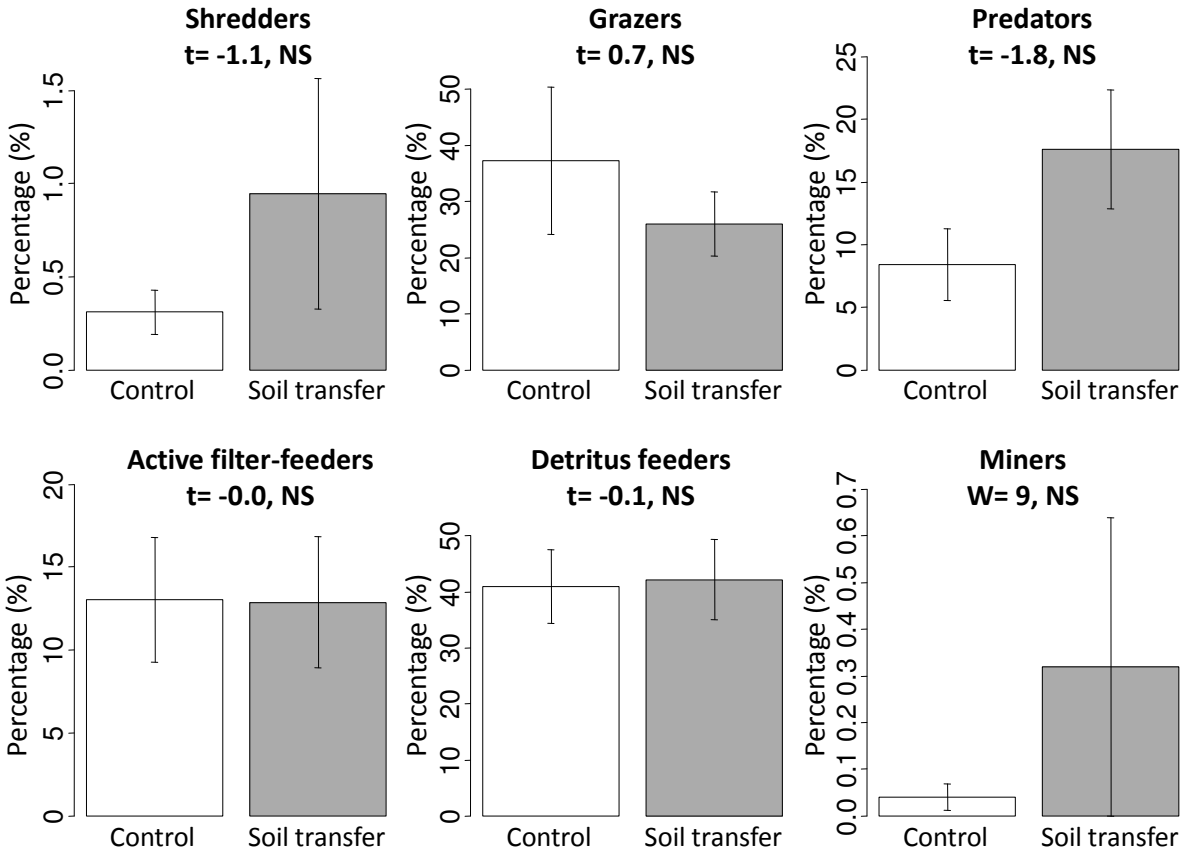

Figure 3.2.7: Mean and standard errors of the percentage of the different functional feeding guilds in the control blocks (white, n=4) and in the soil transfer blocks (grey bars, n=4). The t of Student tests or the W of the Wilcoxon tests performed are shown above the bars (NS: non significant).

3.2.3.3. Comparison with natural temporary wetlands

No significant difference was observed in the Jaccard similarity indices between the two treatments and the natural community, and we observed high similarity indices with the natural community for both soil transfer and control blocks (0.74±0.01 and 0.76±0.02; ***Figure 3.2.8***).

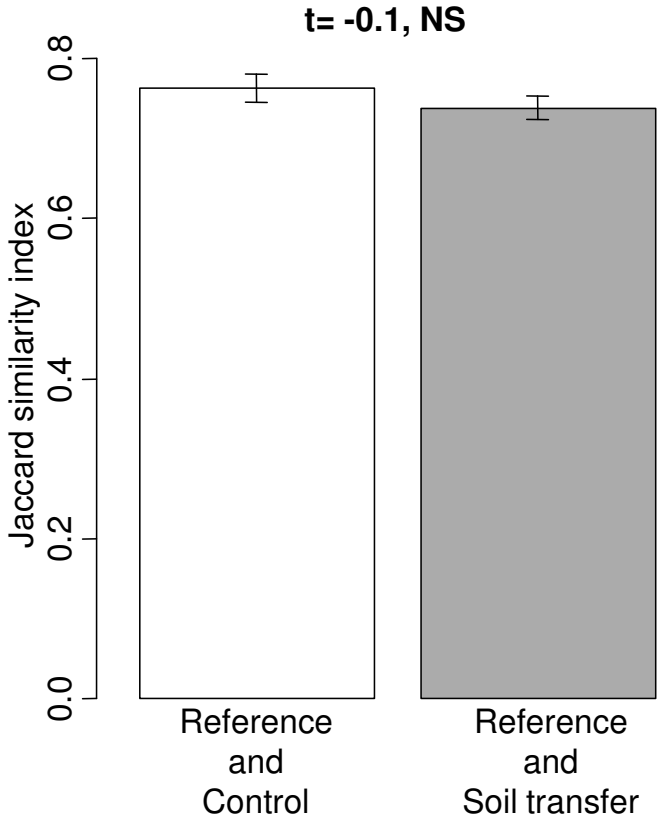

Figure 3.2.8: Mean and standard errors of Jaccard similarity index between the natural community and the control blocks (white, n=4) and the soil transfer blocks (grey bars, n=4). The t of Student tests performed are shown above the bars (NS: non significant).

3.2.4. Discussion

3.2.4.1. Effect of soil transfer on invertebrate communities

Many invertebrates have the potential to disperse and colonize new habitats if the proper habitat is provided (Jenkins and Underwood 1998; Keesing and Wratten 1998; Green and Figuerola 2005). Zooplankton, which are not adapted for migrating, depend only on the following vectors for passive dispersal: wild boar (Vanschoenwinkel et al. 2008), waterfowl (Figuerola and Green 2002a), amphibians (Bohonak and Whiteman 1999), nutria (Waterkeyn et al. 2010), and aquatic insects (Van de Meutter et al. 2008), all of which play an important role in the natural dispersal of zooplankton. The present study has shown that with soil addition, the abundance of zooplankton significantly increases. Soil transfer also was also found to significantly increase the species richness of macrophytes and of the aquatic vegetation cover (***Chapter 3.1***). Other studies dealing with soil transfer in wetland restoration showed a beneficial effect on zooplankton and

aquatic plants (Brown and Bedford 1997; Brown et al. 1997; Brady et al. 2002; Tong et al. 2013), due to dormant aquatic plant seeds and invertebrate eggs residing within the wetland sediments. This strategy of persisting in resting stages is essential in temporary wetlands where the dry phase is considered as a disturbance (Bonis 1998) and the production of dormant propagules is a way of persisting and be resilient.

By improving macrophytes and zooplankton communities, we expected an increase in macroinvertebrate communities. Indeed, as the components of ecosystems have complex linkages to each other, changes in one component may lead to cascading changes in the whole system. It had been demonstrated that vegetation affects macroinvertebrate composition by providing food and protection from predators (Vince et al. 1976; Rozas and Odum 1988; Heck and Crowder 1991; Peterson and Turner 1994; Xingzhong et al. 2005; Stewart and Downing 2008; Tong et al. 2013). Vegetation can also lead to higher frequencies of reproduction events where better habitats provide better protection. Moreover, the higher abundance of zooplankton may lead to a change in the functional-feeding composition, accompanied by an increase in prey. However, in this study we found no clear macroinvertebrate composition change with soil transfer and no difference in functional-feeding guilds, even we observed a trend with more predators in soil transfer blocks, and no difference in larval stage abundance among treatments. Only one coleopteran taxon was significantly more abundant in the soil transfer blocks. Although the statistical analyses did not detect any differences, there were 5 species only found in soil transfer blocks that were entirely absent from the control group. Among them, a gastropod, which does not have an aerial stage, had probably been dispersed by the soil transfer.

In contrast to zooplankton, macroinvertebrates are highly mobile and can choose their habitat: temperature, salinity, and habitat structure are important determinants of whether species colonize a habitat. Despite this, our study has shown that colonization of macroinvertebrates is not only related to habitat quality but is also a function of stochastic dispersal processes. Moreover, even if macrophytes and zooplankton abundance can improve habitat quality, the effect may be insufficient to attract more macroinvertebrates. Similar results were observed with hay transfer in grassland restoration, where grasshoppers were transferred by hay but were not able to establish

permanently due to poor habitat quality on the former arable field during the initial restoration stages (Kiehl and Wagner 2006).

The absence of a change macroinvertebrate abundance between treatments may be partially explained by the absence of fish in the blocks. With any predator risk, the predator protection provided by macrophytes does not play a role in macroinvertebrates habitat selection. Another partial explanation could be isolation. Indeed, connectivity, habitat linkage, and landscape are important for colonization. If the restored wetland is far from a natural "source population", colonization may occur slowly. Restoring or creating marshes in close proximity to natural marshes should accelerate the development of invertebrate communities (Sacco et al. 1994). The existence of a nature reserve containing temporary wetlands less than 1 km away makes dispersal processes possible. Wetland size can also have a limiting effect on natural macroinvertebrate colonization (Eitam et al. 2004) . Finally, long-term monitoring can also improve the response of macroinvertebrate communities to soil transfer. This effect is demonstrated by the significant correlation between taxa richness of restored sites and time since restoration (LaSalle et al. 1991; Posey et al. 1997; Dodson and Lillie 2001; Muotka et al. 2002).

The present study has shown that soil transfer does not change the richness of the zooplankton and macroinvertebrate community. With regard to abundance, it has been shown that soil transfer does provide assistance to many non-aerial invertebrates and can result in an invertebrate community that is dominated by non-aerial invertebrates. At the same time, we did not observe enhanced similarity to natural wetland in the soil transfer blocks; rather they exhibited an overall similarity index that was nearly identical to that of the control block. This is in contrast to previous studies in which soil transfer resulted in elevated similarity to the natural community together with greater diversity of zooplankton and macroinvertebrates (Brown and Bedford 1997; Brown et al. 1997; Brady et al. 2002; Tong et al. 2013). This study leads us to ask the need of soil transfer to restore invertebrate community.

The approach used in this paper to quantify invertebrate recruitment after wetland creation suffers from a number of pitfalls, which can explain the absence of any difference in similarity index between treatments. The low number of replicates can

explain the weak statistical results. The taxonomic levels of zooplanktons were not very precise, limiting the detection of differences between control and soil transfer treatments.

3.2.4.2. Implication for restoration: choose of indicators success

Even when invertebrates have dispersal ability, the aim of favoring their colonization with soil transfer is to avoid unwanted succession stages and to facilitate their colonization with a "jump start" (Brady et al. 2002). Indeed, succession is dictated in part by dispersal abilities, by suitable habitat, and also by species interactions and succession stages, and the presence of a dominant competitor could affect the succession sequence (Jenkins and Underwood 1998). Moreover, by using soil transferred from several donor sites, we may increase species richness in the soil. A consequence of introducing a diverse egg bank is a storage effect, promoting the coexistence of competing species in a temporally variable environment (Chesson 1985). This dormant reservoir is a powerful mechanism for maintaining species diversity within communities by promoting the coexistence of a greater number of species. Because the technique did not achieve the restoration goals of this study, we propose, as has also been suggested by various other authors (Levin et al. 1996; Keesing and Wratten 1998; Brady et al. 2002), to collect and directly transfer individuals of threatened taxa, charismatic taxa, or taxa with low dispersal to the restored wetland. Soil transfer has the advantage of being able to handle not only invertebrate eggs but also macrophytes propagules, which means it can be more efficient and less expensive.

However, even though our study does not recommend active restoration for invertebrate communities, we have certainly highlighted the importance of using multiple indicators to assess restoration success. Previous studies have observed differences between floristic data and fauna such as grasshoppers (Andersen et al. 2001; Wagner 2004; Kiehl and Wagner 2006) and koala (Cristescu et al. 2013), with regard to the response to restoration measures. The observed differences indicate that the faunal compartment does not directly reflect the flora. Flora-only based assessment of restoration success may not accurately assess fauna recolonization. Indeed, the soil transfer technique itself appears very efficient at restoring plant communities while being

markedly unhelpful in restoring invertebrate communities (***Chapter 3.1***), because spontaneous colonization appears more rapid for invertebrate. Invertebrates have been recognized as efficient indicators of ecosystem functioning, and because ecological restoration should have the goal of recreating the integrity of an ecosystem (National Research Council 1992), one should not only monitor plants and abiotic parameters but also fauna. Moreover, macroinvertebrate and zooplankton can be used as reliable indicators of restoration impacts (Ilmonen et al. 2013).

The choice between monitoring plants and monitoring fauna will ultimately be decided by weighing cost and efficiency. Increasing the number of indicators leads necessarily to higher costs. However, as recommended by Cristescu and coauthors (2013), fauna species should be directly monitored to ensure the recolonization of 1) species of interest and 2) fauna involved in the long-term resilience of the ecosystem. At least, if restoration projects cannot take in account other compartments than plants, the present study has shown us to at least be extremely cautious about the interpretation of a part of the restoration that does not reflect the nature of the entire ecosystem.

Transition to Chapter 4

The objectives of ***Chapter 4*** are to find out if it is possible to restore a low productive species-rich ecosystem after cultivation and amendments, and to determine if, as it is demonstrated in the ***Chapter 3.1*** for aquatic plant communities, the dispersion and the abiotic filter play the more important roles in plant community assembly.

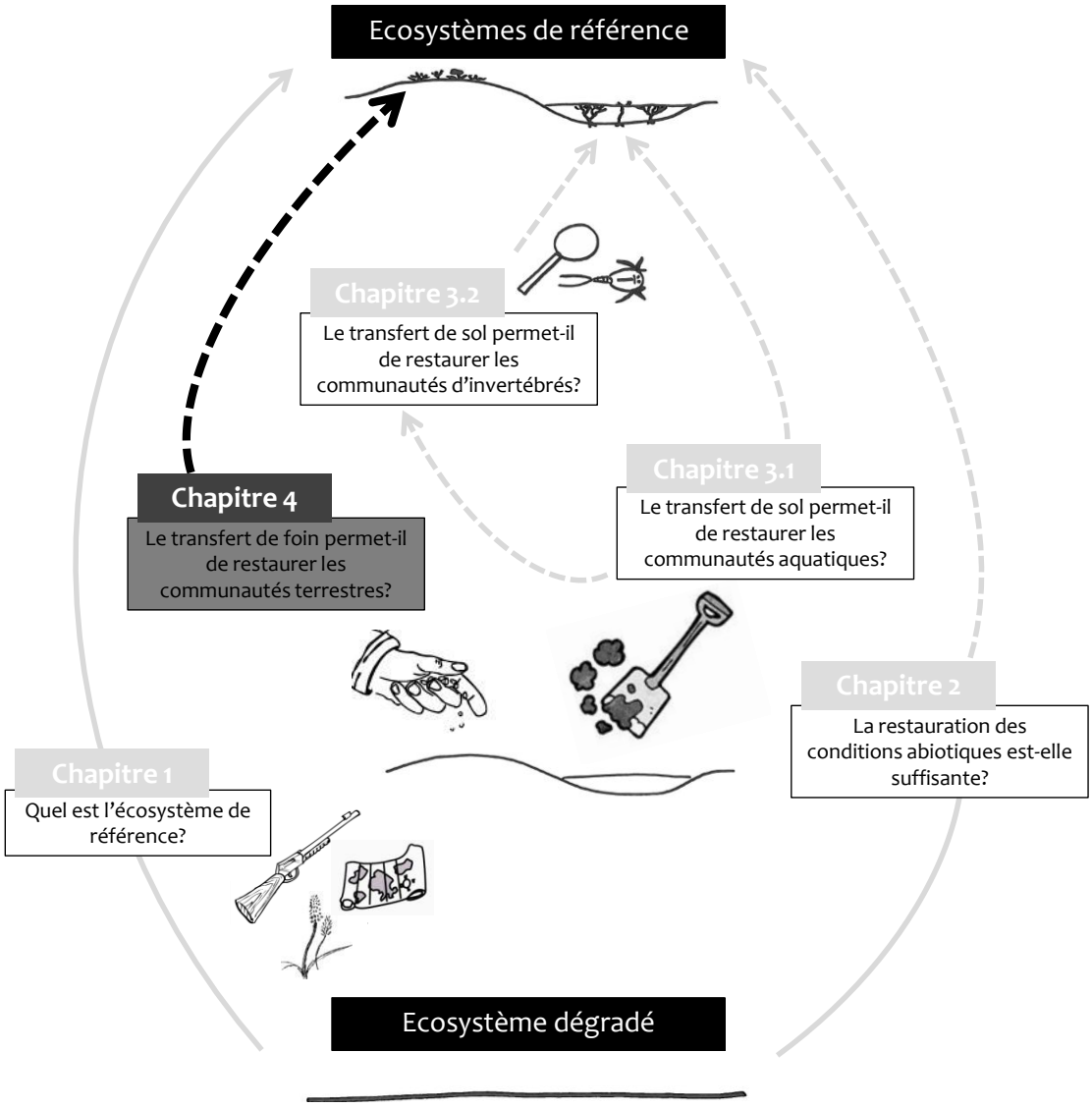

Figure T4.1: Location of ***Chapter 4*** in the general thesis organization

T.4.1. Difference between invertebrate and plant colonization

Chapter 3.1 and ***3.2*** shows contrasted results between plant and invertebrate spontaneous colonization (i.e. in control blocks). The similarity index between reference

and control block was higher for the invertebrate community (0.74±0.01) than for the plant community (0.19±0.06), indicating that recolonization appears more rapid for invertebrates. The reasons for this might be that invertebrates have shorter life cycles, some may be autogamous (no need to introduce the two sexes simultaneously) and most macro-invertebrates are mobile in at least one stage of their life cycle.

T.4.2. Plant material choice for grassland restoration

To restore temporary wetland a community, soil transfer was used (***Chapter 3.1***). However for terrestrial ecosystems, soil transfer involves the destruction of the donor ecosystem (Vécrin and Muller 2003; Jaunatre et al. 2012) and another material must be used. The objective of ***Chapter 4*** is to test hay transfer for grassland community restoration.

Plant materiel gathering in a meso-xeric grassland using a leaf blower on the vacuum position

Plant material establishment on plant material transfer block (*Trifolium resupinatum*, *Brachypodium distachyon*, *Filago pygmaea,* and *Scorpiurus muricatus*)

Chapter 4 - Effect of topsoil removal and plant material transfer on vegetation development in created Mediterranean meso-xeric grasslands

Isabelle Muller, François Mesléard & Elise Buisson

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4.1. Introduction

In the coastal deltaic zones of the Northern Mediterranean region, meso-xeric grasslands are mainly located on fluvial strips and relict dunes. In the Camargue area (Rhône delta), this habitat has the highest plant richness characterized by a high proportion of annuals (Molinier and Tallon 1970; Braun-Blanquet 1973) and is widely used by rare and protected fauna (Guillaume 1975). These grasslands are traditionally managed by extensive on-and-off livestock grazing throughout the year, maintaining habitats open and enhancing biodiversity (Mesléard et al. 1991). Without this extensive grazing, they are colonized by *Phillyrea angustifolia* L., leading to a decrease in species richness due to the dense vegetation (Mesléard et al. 1991; Mesléard et al. 2011). They are also the most threatened habitat, essentially because of cultivation expansion (Lemaire et al. 1987). Thus, meso-xeric grasslands are included as a priority habitat (code 6220) in the European Union Habitats Directive (European Commission 1992). Since World War II, these grasslands have drastically declined locally from around 4000 ha to less than 2000 ha fragmented in small units (Mesléard et al. 2011).

Nowadays, changes in agricultural activities and the local abandonment of land devoted to crop cultivation provide opportunities to implement restoration projects. In this context, restoration of suitable habitats for target species has been promoted as a conservation strategy. Restoration consists of guiding degraded ecosystems towards target ecosystems by accelerating or by passing the intermediate stages of succession, recreating favorable abiotic and biotic conditions which allow recolonization by native species (Bakker et al. 1996; Society for Ecological Restoration 2004).

One of the primary factors limiting the success of restoration is often the lack of available target seeds because of depleted seed banks and limited seed dispersal from the surrounding landscapes (McDonald 1993; Hutchings and Booth 1996; Bakker et al. 1996; Pärtel et al. 1998; Bischoff 2002; Münzbergová and Herben 2005; Bossuyt and Honnay 2009). Several studies have demonstrated that target vegetation is likely to be restored when the area to restore is adjacent to natural vegetation (Mesléard et al. 1999; Prach et al. 2001b; Řehounková and Prach 2007; Prach and Hobbs 2008; Lencová and Prach 2011; Jírová et al. 2012) or when a relictual seed bank is present (Mesléard et al. 1995; Willems and Bik 1998). However, when the site has been subjected to a long

cultivation period, target vegetation cannot establish through spontaneous colonization (Prach et al. 2001b) and an input of diaspores is required (Hutchings and Booth 1996; Bischoff 2002; Cramer et al. 2008; Prach and Hobbs 2008; Török et al. 2011b; Hölzel et al. 2012). Indeed, agricultural practices can influence plant communities by fertilization (Bakelaar and Odum 1978; McLaughlin and Mineau 1995; Bobbink et al. 1998), ploughing (Gibson and Brown 1992; Clements et al. 1996; Sutcliffe and Kay 2000; Dutoit et al. 2004) and water management (Burel et al. 2008). Plant material transfer is one possible method of re-introducing target communities. Several studies indicate that seed limitations can be overcome successfully by plant material transfer in various situations, such as in heathland (Pywell et al. 2011), in fen meadow (Patzelt et al. 2001; Klimkowska et al. 2010b), flood-plain meadow (Vécrin et al. 2002; Hölzel and Otte 2003; Donath et al. 2007), or grassland restoration (Edwards et al. 2007; Kiehl et al. 2010; Coiffait-Gombault et al. 2011; Török et al. 2012).

The abiotic and biotic conditions of the site to be restored potentially represent other key factors determining the success of restoration. In former agricultural lands where upper soil layers contain high levels of nutrient (Marrs 1985) favoring most of the ruderal species of the seed bank (Davy 2008; Török et al. 2011a) and increasing competition (Marrs 2002), the establishment of oligotrophic grasslands may be compromised despite seed addition (Gough and Marrs 1990; Pywell et al. 2003). In the process of community assembly described by the filter model (Keddy 1992; Lortie et al. 2004; Guisan and Rahbek 2011), overcoming the dispersion filter may not be sufficient; establishment limitation of transferred seeds can be caused by two other filters: the environmental conditions and competition. Indeed, the successful restoration of low-productive grasslands, such as meso-xeric grasslands, is strongly hampered by abiotic and competition constraints. When recruitment (regional processes) is accelerated by plant material transfer, local processes, such as competition, play a role in plant composition (Klimkowska et al. 2010b); competition is an important biotic interaction in former agricultural land, because weed species are successful competitors more adapted to post-cultivation abiotic conditions (Török et al. 2011a). To overcome the stage with the dominance of these competitive species, topsoil removal has been shown to facilitate restoration, by removing the seed bank inherited from the agricultural period and by impoverishing

nutrient soil content (Aerts et al. 1995; Patzelt et al. 2001; Tallowin and Smith 2001; Hölzel and Otte 2003; Allison and Ausden 2004; Buisson et al. 2006b; Buisson et al. 2008; Kiehl et al. 2010; Klimkowska et al. 2010b; Török et al. 2011b; Jaunatre et al. 2012).

Previous studies (Patzelt et al. 2001; Hölzel and Otte 2003; Kiehl and Wagner 2006; Rasran et al. 2007; Klimkowska et al. 2010b) showed the benefits of the combination of topsoil removal and plant materiel transfer in different types of plant communities. In this study, we tested the restoration of a low-productive meso-xeric grassland. We thus used experimental on-site blocks to know if topsoil removal and plant material transfer are sufficient to allow the establishment of the less competitive and stress-tolerant target species. The aim is to identify future treatments suitable for application to a larger area (several hectares). In order to reduce the impact of cultivation on sites, characterized by nutrient-rich soils and by a soil seed bank containing undesirable species, we used topsoil removal and plant material transfer in combination. To assess the potential role of the present soil seed bank (i.e. inherited from cultivation) on vegetation establishment, we tested two depths of topsoil removal. We hypothesized that increasing topsoil removal would lead to a diminution of the soil seek bank (i.e. depletion with depth) (Grillas et al. 1993; Bonis and Lepart 1994; Bonis et al. 1995; Hölzel and Otte 2003; Rasran et al. 2007; Klimkowska et al. 2010b) allowing improved target species establishment. The objectives were to test: (1) the effect of two depths of topsoil removal on soil seed bank inherited from the cultivation period; to do so, we assessed, in the greenhouse, the emergence of the seed bank from soil samples taken at soil surface (0 to 5 cm deep) and at two different depths of topsoil removal (5 to 20 cm deep and 20 to 40 cm deep); (2) the effect of two depths of topsoil removal on vegetation establishment; (3) the effect of plant material transfer on vegetation establishment; and (4) the combined effect of two depths of topsoil removal on the success of plant material transfer; to do so, we monitored vegetation dynamics on permanent plots with four different treatments: 5 cm topsoil removal, 20 cm topsoil removal, 5 cm topsoil removal with plant material transfer and 20 cm topsoil removal with plant material transfer.

4.2. Materials and methods

4.2.1. Study site

The experiment was conducted in the Cassaïre site (c. 43°31' N, 4°44' E, 3 m maximum elevation) located east of the Camargue area (Rhône delta, Southern France, ***Figure 4.1***). The climate is typically Mediterranean, characterized by an annual average temperature of 15°C, an annual rainfall of 550 mm mainly concentrated in autumn, and a summer drought.

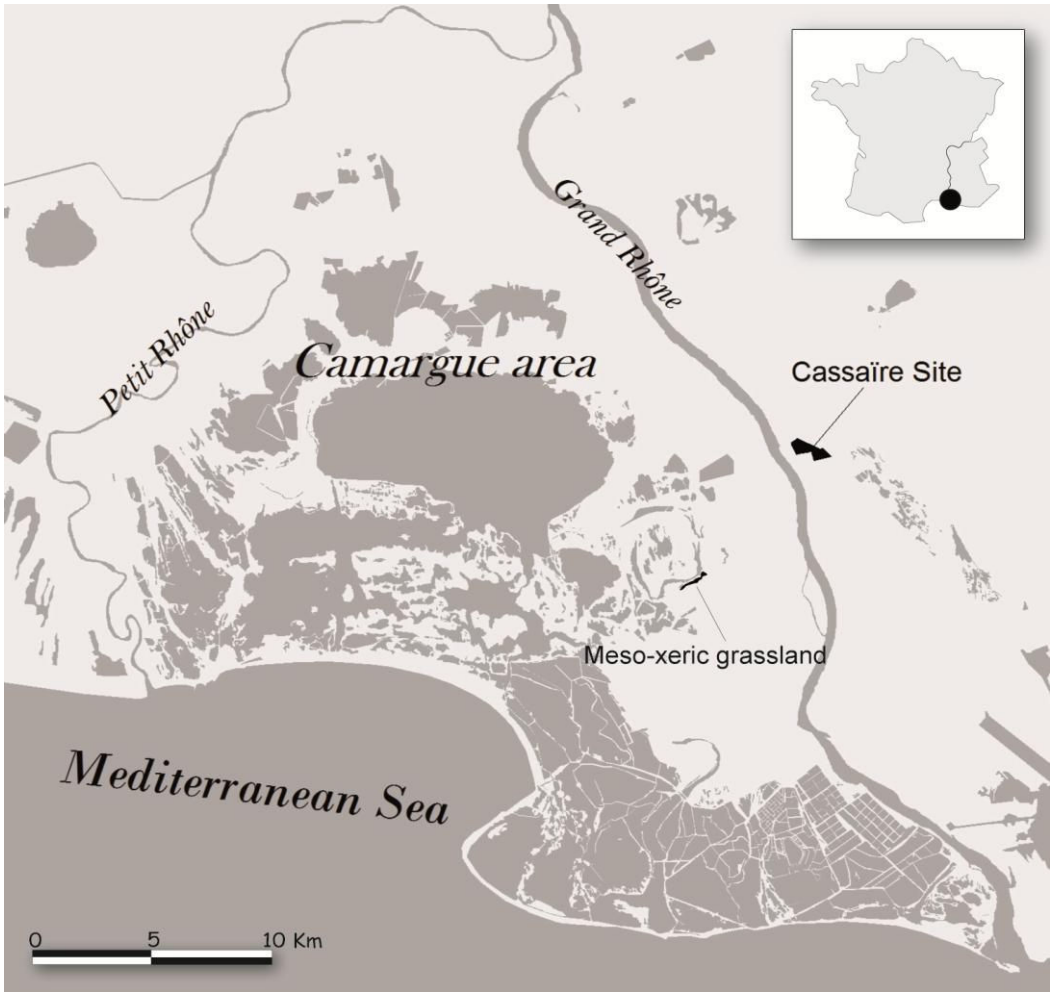

Figure 4.1: Location of the Cassaïre site (in black) and of the meso-xeric grassland corresponding to the reference grassland (in black). The grey shading indicates the wetlands of the Camargue area.

For more than 60 years, the study site has been subject to rice cultivation which definitively stopped in 2004. The technical agricultural itinerary of rice cultivation includes plowing to a 20 cm depth in winter, soil leveling and fertilization before impoundment and planting in April for a harvest in September (Marnotte et al. 2006).The site has been

submitted to recurrent leveling for rice cultivation since the 1940's, leading to the complete elimination of the natural topography.

The reference grassland, one of the largest remaining meso-xeric grasslands (30 ha) in the Camargue area, is located in the Tour du Valat reserve (Otero and Bailey 2003), which is about 5 km away from the Cassaïre site (c.43°29' N, 4°40' E, **Figure 4.1**). It is characterized by a high diversity, composed of *Brachypodium phoenicoides* (L.) Roem. & Schult., *Brachypodium distachyon* (L.) P. Beauv., *Scorpiurus muricatus* L., *Psilurus aristatus* (Gouan) Schinz & Thell., *Filago pygmaea* L., *Filago vulgaris* Lam., *Galium murale* (L.) All., *Euphorbia exigua* L., *Dactylis glomerata* subsp. *hispanica* (Roth) Nyman, *Crepis sancta* (L.) Bornm. and *Crepis vesicaria* L.. The reference grassland is managed by traditional extensive on-and-off livestock grazing (Mesléard et al. 2011).

The present study concerns experiments conducted in 2010 with the aim of identifying future treatments suitable for application on a large scale. This required that ten blocks with a gentle slope be dug (15 m long × 5 m wide × 40 cm deep at the deeper end, **Figure 4.2**) on the site in December 2010. They were arranged by randomly disposed groups of two (five groups in total). The slopes of these blocks (10 m long × 5 m wide) were used for this experiment.

In order to investigate soil properties at various depths of topsoil removal in the Cassaïre site, and to compare with surface soil of the reference grassland, we randomly collected in autumn 2011 soil samples composed of 3 pooled sub-samples: five soil samples from the surface Cassaïre site (0-10 cm), five from 40 to 60 cm deep, and four from the surface the reference grassland (0-10 cm). Samples, composed of one liter of soil, were dried and sieved (at 200 µm). Soil analyses were conducted by the soil analysis laboratory of the INRA (The French National Institute for Agricultural Research, Aras, France).

4.2.2. Plant material gathering

The reference grassland was used as a donor site for plant material. To enhance species diversity in seeds, plant material was gathered using two techniques, commonly used for gathering plant material for small seeding areas, at various periods:

- the meso-xeric grassland seeds were collected using a leaf blower on the vacuum position in mid-May, mid-June and mid-July 2010 (vacuum harvested material)
- the meso-xeric grassland vegetation was cut with a scythe and raked in mid-May 2007, mid-May 2008 and in the beginning of September 2010 (hay)

We stored this plant material dry in 4°C until the transfer to the Cassaïre site.

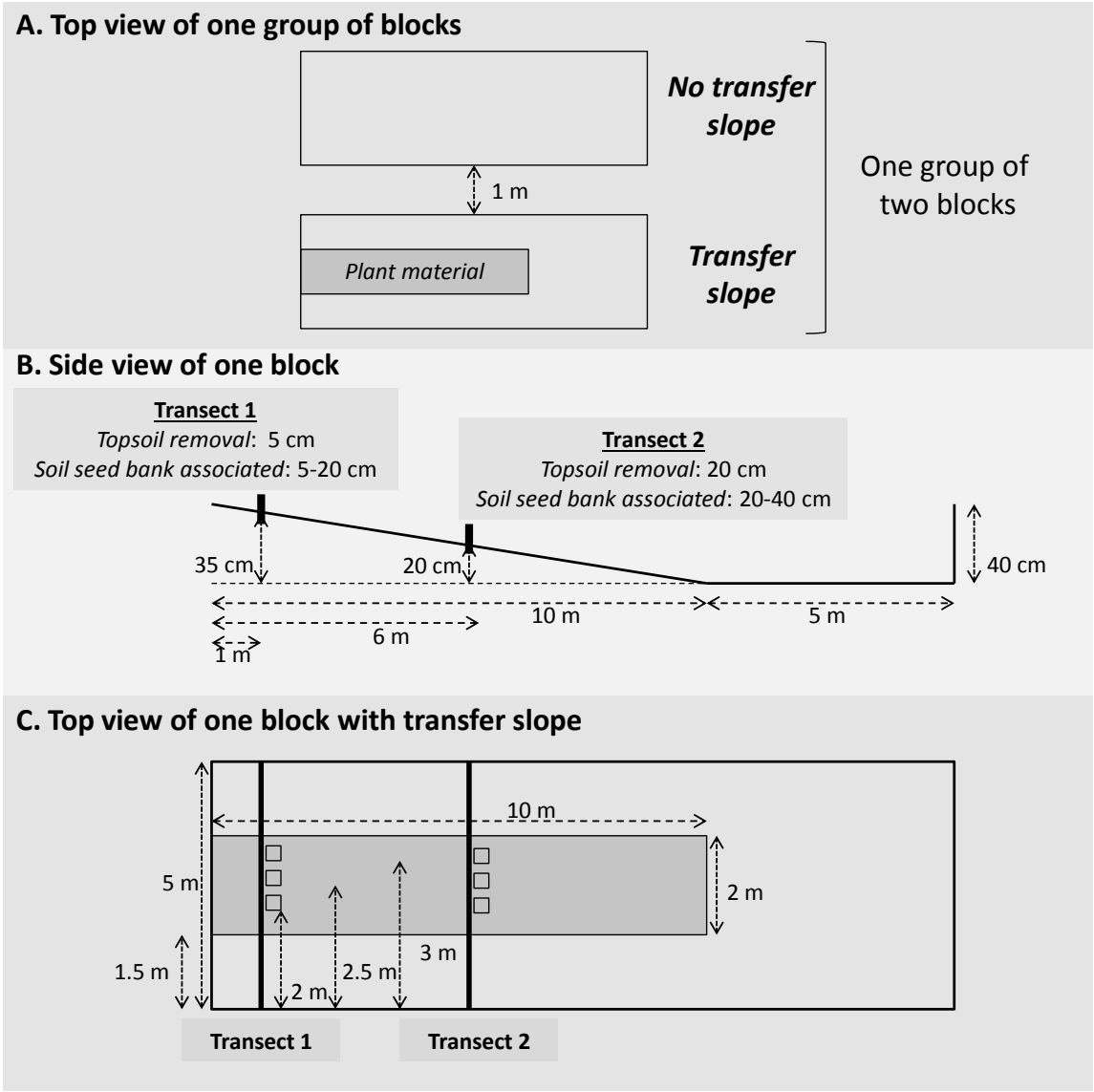

Figure 4.2: Experimental design of A) one group of blocks (five in total), B) side view of one block with the two monitoring transects and C) the top view of one block with transfer slope, the 30 × 30 cm monitoring plots are shown. The grey color shows zone where plant material was spread.

Vegetation monitoring in this reference grassland was carried out beginning in 2001 at the beginning of May (Damgaard et al. 2010), in three randomly distributed permanent 40 × 40 cm plots. In each permanent plot, a set of two crossing lines was established to

indicate 36 pins set on a 3 cm pitch. Species presence was recorded on each of the 36 pins in order to compute the species frequency, the total vegetation cover (%) and species richness in 40 × 40 cm plots were also estimated in all plots. To evaluate the fluctuation in vegetation in response to strong potential climate variations over the years, we performed a Correspondence Analysis (Greenacre 1984) on the reference vegetation data from 2007 to 2012 (the years the plant material was sampled, ***Figure 4.3.A***), we compared species richness (***Figure 4.3.B***) and total cover of vegetation (***Figure 4.3.C***) between years. We observed no obvious changes in plant community composition during these 6 years (***Figure 4.3***).

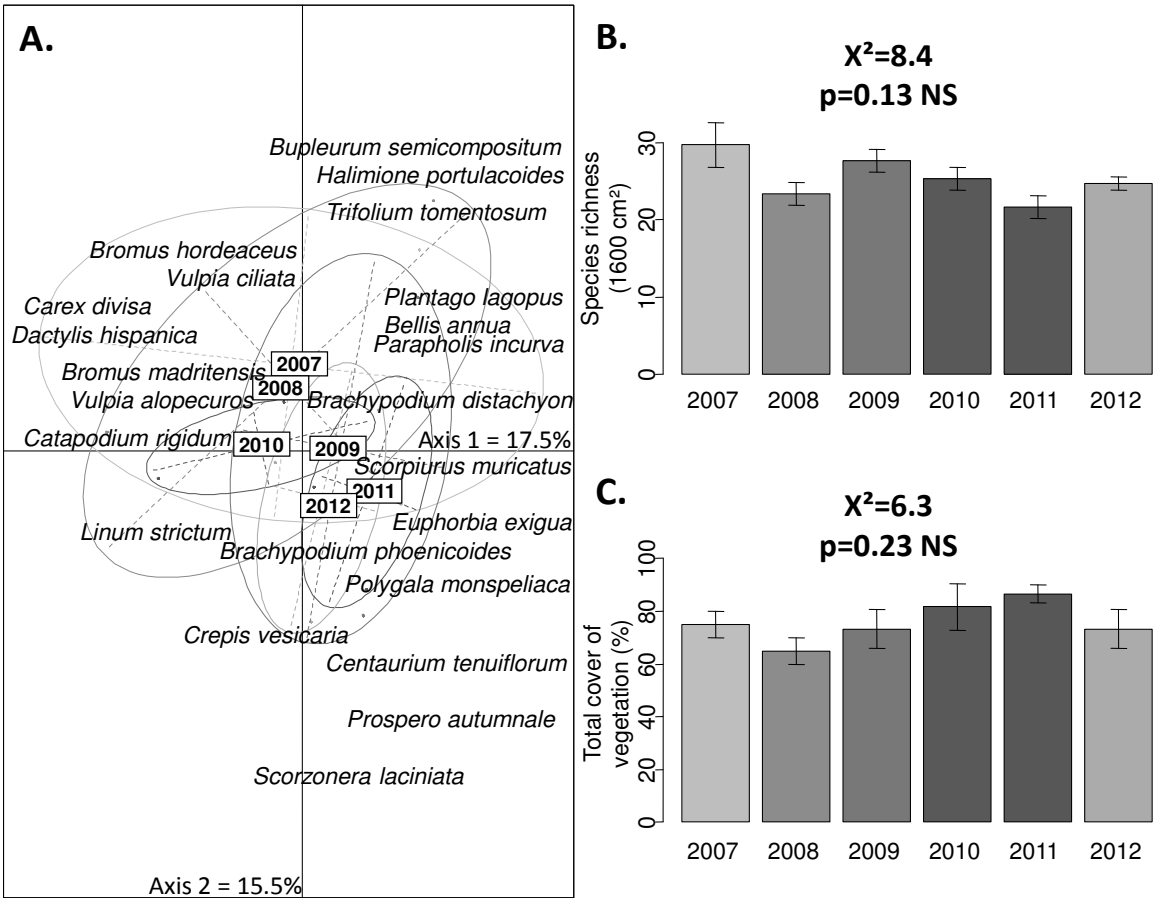

Figure 4.3: A) Ordination plot of the Correspondence Analysis based on species abundances (18 plots × 47 species) on the reference grassland grouped by years, 2007 to 2012. Ellipses are centered on the barycentre and their forms are weighted by the distribution of all points corresponding to the same year. B) Mean and standard errors of species richness (1600 cm²) of the reference grassland in 2007 to 2012. C) Mean and standard errors of total cover of vegetation on 1600 cm² (%) of the reference grassland in 2007 to 2012. The χ^2 and *p*-value of Kruskal-Wallis tests performed are shown above the bars (NS: non-significant). In the interests of clarity, only the 23 species with the higher contributions to axis are shown.

4.2.3. Restoration treatments

In order to test the effect of topsoil removal and plant material transfer on the establishment of plant communities, plant material was spread along the slope (**Figure 4.2**) of one of the two blocks of each group in January 2011 on a day without wind. Vacuum harvested material were spread first, then hay, which, as it is heavier, allowed reducing seed loss by strong winds, improving moisture conditions, and reducing temperature variations. For the five slopes where plant material was transferred (the five transfer slopes), 100 g of vacuum harvested material and 215 g of hay were applied manually on the 2 m × 10 m area (plant material density= 15.75 $g.m^{-2}$, corresponding to a donor area to transfer area ratio of 10:1; **Figure 4.2**). Before spreading, the soil was lightly harrowed perpendicularly to the slope, to aerate the soil so as to provide better conditions for germination. The same operation was done on the other slope of each block group where no plant material transfer was applied (the five no transfer slopes). To limit the abundance of competitive species and to mimic the effects of the grazing that these grasslands are typically subject to we mowed and exported the vegetation in and around the blocks in January 2012 and in January 2013.

4.2.4. Plant material content

To assess the composition (richness and species abundance) of the plant material collected, the same material that was spread on the slopes was also spread in a greenhouse. Three samples of 100 g of vacuum harvested material and 215 g of hay were spread in February 2011 in 30 x 20 cm trays filled with a substrate composed of 50% organic soil and 50% vermiculite (inert substrate) coated with 100 micron medical gauze, to prevent the seeds from sink into the substrate. Each plant material sample was spread on the medical gauze and was distributed among 3 trays in order to have a fine plant material layer which is maximally conducive to seed germination. Trays were watered regularly and rotated with each other several times during the ten months germination period to ensure homogeneous germination conditions for all samples. Germinated seedlings were identified, counted and removed every week to allow germination of other seeds. Unidentifiable plants were transferred to pots and grown until they could be identified.

4.2.5. Vegetation monitoring

Vegetation monitoring was carried out along two permanent transects on each slope (***Figure 4.2***), one at 1 m from the top of the slope (transect 1, corresponding to 5 cm depth topsoil removal) and one at 6 m from the top, the middle of the slope (transect 2, corresponding to 20 cm depth topsoil removal). The vegetation survey was carried out using 30 × 30 cm permanent plots subdivided into nine 10 × 10 cm cells (according to the high species richness and the small minimal area, small plot sizes are usually used in the Camargue area to monitore the Mediterranean meso-xeric grasslands, (Damgaard et al. 2010)). Three plots were distributed along each transect (***Figure 4.2.C***). Presence/Absence of all species was recorded in each cell and a frequency was calculated for each species in each plot. The total vegetation cover (%) was also estimated in all plots. Plots were monitored in mid May 2011 (four months after the transfer), in mid May 2012 (16 months after transfer) and in mid May 2013 (28 months after transfer). In order to compare the vegetation between the various treatments and the reference grassland with the same vegetation monitoring, twenty 30 × 30 cm permanent plots (also subdivided into 10 x 10 cm cells) randomly distributed on the reference grassland were monitored mid May 2010. We used the national code of nomenclature of names for the species (Gargominy et al. 2013).

To analyze the restoration success of communities, among the all species found (***Appendix 2***), we arranged the species into two categories:

1. Meso-xeric grassland target species : present at the reference grassland, corresponding to the characteristic flora of meso-xeric grasslands (Molinier and Tallon 1970; Braun-Blanquet 1973).

2. Non-target species: Arable weeds, ruderal or mesophyllous meadow species germinating from the soil seed bank resulting of the agricultural past and the intensive amendments or resident in the Cassaïre site (e.g. *Rumex crispus* L., *Symphyotrichum subulatum* var. *squamatum* (Spreng.) S.D.Sundb. or *Trifolium repens* L.); they are usually absent from the reference grassland or species with a wide ecological range (e.g. *Lysimachia arvensis* (L.) U.Manns & Anderb., *Bromus madritensis* L. or *Sonchus oleraceus*

L.); some may be found in the reference grassland but are not considered as target species.

4.2.6. Cassaïre seed bank sampling

In order to determine the influence of topsoil removal on the soil seed bank and the potential role of buried seeds in succession in the Cassaïre, we randomly collected 12 soil samples i) from the surface (0 to 5 cm deep), ii) from 5 to 20 cm deep (corresponding to the first transect) and iii) from 20 to 40 cm deep (corresponding to the second transect) (***Figure 4.2***). For each sample composed of 3 pooled sub-samples, 1 L of soil was taken in January 2011 and the soil seed bank was described using the seedling emergence with sample concentration method for ten months (Ter Heerdt et al. 1996). Each sample was cleaned with water in a 200-micron sieve in order to separate the seeds from the clay before spreading them in 30 x 20 cm trays filled with a 50%/50% mix of organic matter and vermiculite coated 100-micron medical gauze, to prevent the seeds from sinking into the substrate. Germinated seedlings were identified as explained previously for the plant material analysis experiment. Control trays filled with the same substrate and coated with medical gauze were used in order to make sure there was no germination from the organic matter or from accidental seed rain in the greenhouse.

4.2.7. Data analysis

In order to test the effect of the two depths of topsoil removal on soil seed bank, we compared species richness of germinated seeds and number of seedlings between the surface and the two depths of seed bank using analysis of variance (ANOVA) followed by Tukey tests (Sokal and Rohlf 1995). In order to compare the composition of the surface seed bank to the deeper seed banks, we calculated for each sample the mean Bray-Curtis similarity index, based on frequencies (Raup and Crick 1979) between each deeper sample and each surface sample. In order to assess surface seed bank variability, we compared each surface seed bank sample to other surface seed bank samples. An index of zero corresponds to an absence of species in common between the two seed banks, while an index of 1 means that there is a similar seed bank composition. We compared the

means of the Bray-Curtis indices across the three depths using an analysis of variance (ANOVA) followed by Tukey tests.

In order to test the effect of the two depths of topsoil removal on vegetation establishment with or without transfer, we compared species richness, the number of target species and the vegetation mean percent cover between transect 1 and transect 2 of no transfer slopes and transfer slopes for the two year period using the following non-parametric tests: Kruskal-Wallis, followed by pairwise Wilcoxon comparisons with a p-value adjustment according to Holm's method (Holm 1979). To analyze differences between transect 1 and transect 2, we used non parametric multivariate analysis of variance on vegetation data for no transfer slopes and for transfer slopes (nonparametric MANOVA, (Anderson 2001)).

In order to test the effect of plant material transfer on vegetation establishment, we compared the transfer slopes (transect 1 + transect 2), the no transfer slopes (transect 1 + transect 2), and the plant material with the reference grassland. We calculated the Jaccard similarity index based on the presence and absence of species (Jaccard 1901): an index of zero corresponds to an absence of species in common between the treatment (plant material content, no transfer slopes or transfer slopes) and the reference grassland, while an index of 1 means that there is a similar vegetation composition. For each plot surveyed on a slope, the mean Jaccard index between this plot and each plot on the reference grassland was calculated and an average Jaccard similarity index was calculated for each treatment. In order to assess reference grassland variability, we compared each plot of the reference grassland with the others on the reference grassland. When the data were conform to parametric conditions, we used ANOVA, followed by Tukey tests, otherwise, we used a Kruskal-Wallis test, followed by a pairwise Wilcoxon comparison employing a p-value adjustment according to Holm's method, to compare species richness, number of target species richness, and the means of the Jaccard index between treatments (reference grassland, plant material content, transfer slopes and no transfer slopes). To analyze differences between transfer and no transfer slopes, we used nonparametric MANOVA on vegetation data in 2011, 2012 and 2013. We performed a CA based on the presence and absence of species present in at least three

plots in the reference grassland, in the greenhouse plant material, on the transfer slopes in 2013, and on the no transfer slopes in 2013 (83 plots × 94 species).

All tests were performed using R 2.12.0 (R Development Core Team 2010) with a p=0.05 threshold using the "ade4" package (Dray et al. 2007) and the "vegan" package (Oksanen et al. 2008).

4.3. Results

4.3.1. Effects of topsoil removal on soil nutrients

Soil analyses showed significantly lower amounts of total C, organic matter and total N in the Cassaïre deep soil from reference grassland and the Cassaïre surface (***Table 4.1***). P_2O_5 content was significantly lower in the Cassaïre deep, close to P_2O_5 content in grassland reference (***Table 4.1***).

Table 4.1: Mean and standard errors of nutrient contents for the surface soil (0-10 cm) of the reference grassland and of the Cassaïre site and for the soil at 40 cm deep at the Cassaïre site (40-60 cm). Df are the degrees of freedom, χ^2 and p are the chi² value and p-value of Kruskal-Wallis tests. Values on a line with the same letter are not significantly different according to pairwise Wilcoxon multiple comparisons with Holm p adjustment.

	df	*p*-value	Reference grassland		Surface Cassaïre site		Depth Cassaïre site	
Total C (g.kg-1)	2	< 0.05	26.95±7.58	a	19.75±1.08	a	4.81±0.80	b
Total N (g.kg-1)	2	< 0.05	2.46±0.91	a	1.67±0.07	a	0.31±0.05	b
OM (g.kg-1)	2	< 0.05	46.67±13.10	a	34.15±1.86	a	8.31±1.37	b
P2O5 (g.kg-1)	2	< 0.05	0.01±0.00	a	0.09±0.01	b	0.02±0.01	a
CaO (g.kg-1)	2	= 0.17	10.29±0.81	a	9.97±0.16	a	9.51±0.13	a
MgO (g.kg-1)	2	= 1.00	0.48±0.20	a	0.39±0.09	a	0.39±0.08	a
K2O (g.kg-1)	2	= 0.055	0.33±0.12	a	0.34±0.06	a	0.09±0.02	a

4.3.2. Effects of topsoil removal on seeds germinating from the seed bank (greenhouse)

In total 41 species germinated from the soil seed bank (***Appendix 2***), representing a total of 5102 seedlings. The number of seedlings of the soil seed bank declined significantly when going from 0-5 cm and from 5-20 cm of topsoil removal (209±34 per liter without topsoil removal *vs.* 119±19 per liter after 5 cm topsoil removal; ***Figure 4.4.A***).

However no difference was noticed between 5-20 cm and 20-40 cm of soil removal (98±12 per liter; ***Figure 4.4.A***). A removal depth of 5 cm decreased by 43% the number of seedlings and a removal depth of 20 cm decreased by 53% the number of seedlings relative to the surface. The species richness also declined between 0-5 cm and 5-20 cm of topsoil removal (18±0.8 without topsoil removal *vs.* 13±0.9 species per liter after 5 cm topsoil removal; ***Figure 4.4.B***), but no difference was found between the two deeper ranges of removal (13±0.9 species after 20 cm removal depth; ***Figure 4.4.B***).

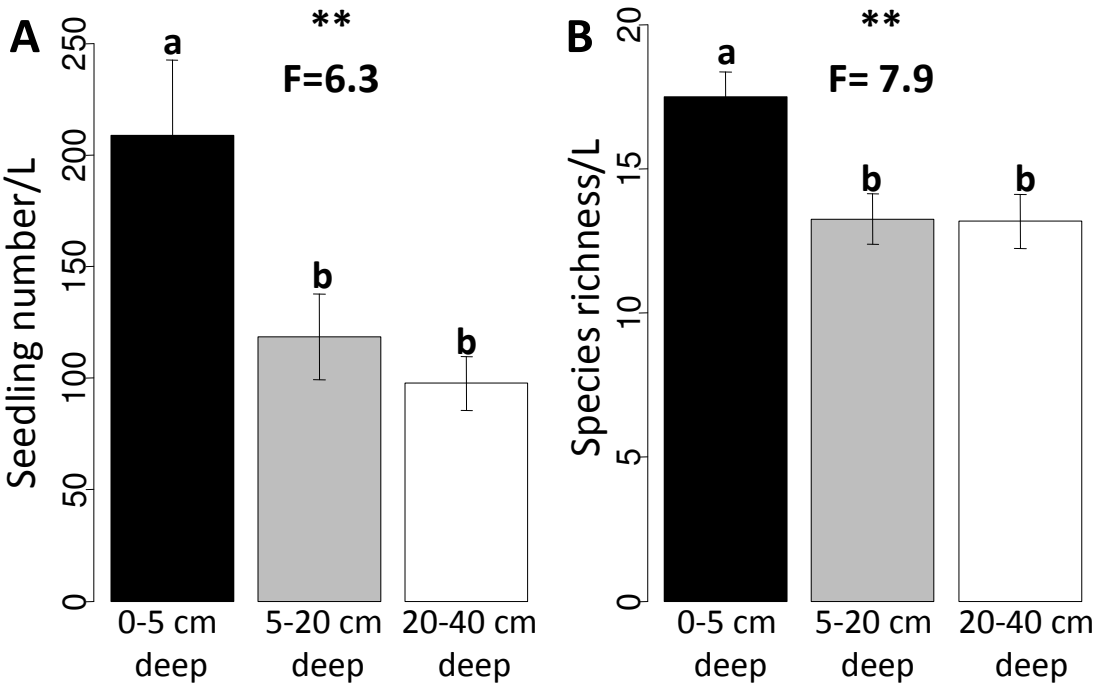

Figure 4.4: Mean and standard errors of A) seedling number of soil seed bank per liter and B) species richness of soil seed bank per liter of the Cassaïre site without topsoil removal (0 to 5 cm deep, black bars, n=12 plots), with 5 cm removal depth (5 to 20 cm deep, grey bars, corresponding to the transect 1, n=12 plots) and with 20 cm removal depth (20 to 40 cm deep, white bars, corresponding to the transect 2, n=12 plots). The F of ANOVA performed are shown above the bars (**: $p<0.01$), bars showing the same letters do not have any significant differences according to Tukey tests.

Seedling emergence composition between the various depths did not differ as indicated the Bray-Curtis similarity index which showed no significant difference between the three depths (Bray-Curtis index in 0-5 cm= 0.95±0.01, Bray-Curtis index in 5-20 cm= 0.95±0.01 and Bray-Curtis index in 20-40 cm= 0.92±0.01, $\chi^2=0.82$, df=2, n=36, p=0.66). In all cases the species richness was characterized by *Juncus bufonius* L. (26%), an amphibian

annual species present on wet sandy substrates in the Camargue area but favored by rice cultivation, *Ammannia χ coccinea* Rottb. (12%), *Lindernia dubia* (L.) Pennell (9%) and *Cyperus difformis* L. (9%) three typical exotic ricefield weeds, and *Trifolium repens* L. (10%). We found 1 seedling each of meso-xeric grassland target species *Plantago coronopus* L., *Trifolium campestre* Schreb., *Carex divisa* Huds., *Medicago polymorpha* L. and *Centaurium spicatum* (L.) Fritsch ex Janch.. No other seedling of target species of meso-xeric grassland was recorded.

4.3.3. Effects of topsoil removal on spontaneous vegetation development: comparing transects on no transfer slopes

Only one target species, *Plantago coronopus* L. present in the soil seed bank, was recorded in the no transfer slopes in 2011 and in 2012 (**Figure 4.5.C**) and the vegetation was significantly different from the reference grassland as determined by species richness, which was lowest in the no transfer slopes ($F=38.4$, df=7, n=203, $p<0.001$; **Figure 4.5.A**) and by the Jaccard similarity index ($\chi^2=113.6$, df=7, n=203, $p<0.001$; **Figure 4.5.B**).

In the first year of monitoring, we found a significant decrease in plant species richness with increasing topsoil removal (11.6±0.6 for transect 1 *vs.* 5.3±0.7 for transect 2, $\chi^2=51.1$, df=11, n=180, $p<0.001$; **Figure 4.6.A**), but we found no difference in vegetation cover (**Figure 4.6.C**). In the second and the third year of monitoring, we found no significant difference in species richness (**Figure 4.6.A**), or in vegetation cover (**Figure 4.6.C**) between the two transects. The MANOVA performed on the species abundances in 2013 indicated no differences between the two transects in no transfer slopes (df=1, $F=1.1$, $p=0.3$). The composition in the no transfer treatment was similar in the two transects, and characterized by mesophyllous species *Polygonum aviculare* L. (9%) and *Trifolium repens* L. (7%) in the first year, by *Lolium rigidum* Gaudin (8%) and *Poa trivialis* L. (6%) in the second year and by *Lotus corniculatus* subsp. *tenuis* (Waldst. & Kit. ex Willd.) Berher (7%) and *Lolium rigidum* Gaudin (6%) in the third year, which are five species present in the soil seed bank and in the Cassaïre vegetation.

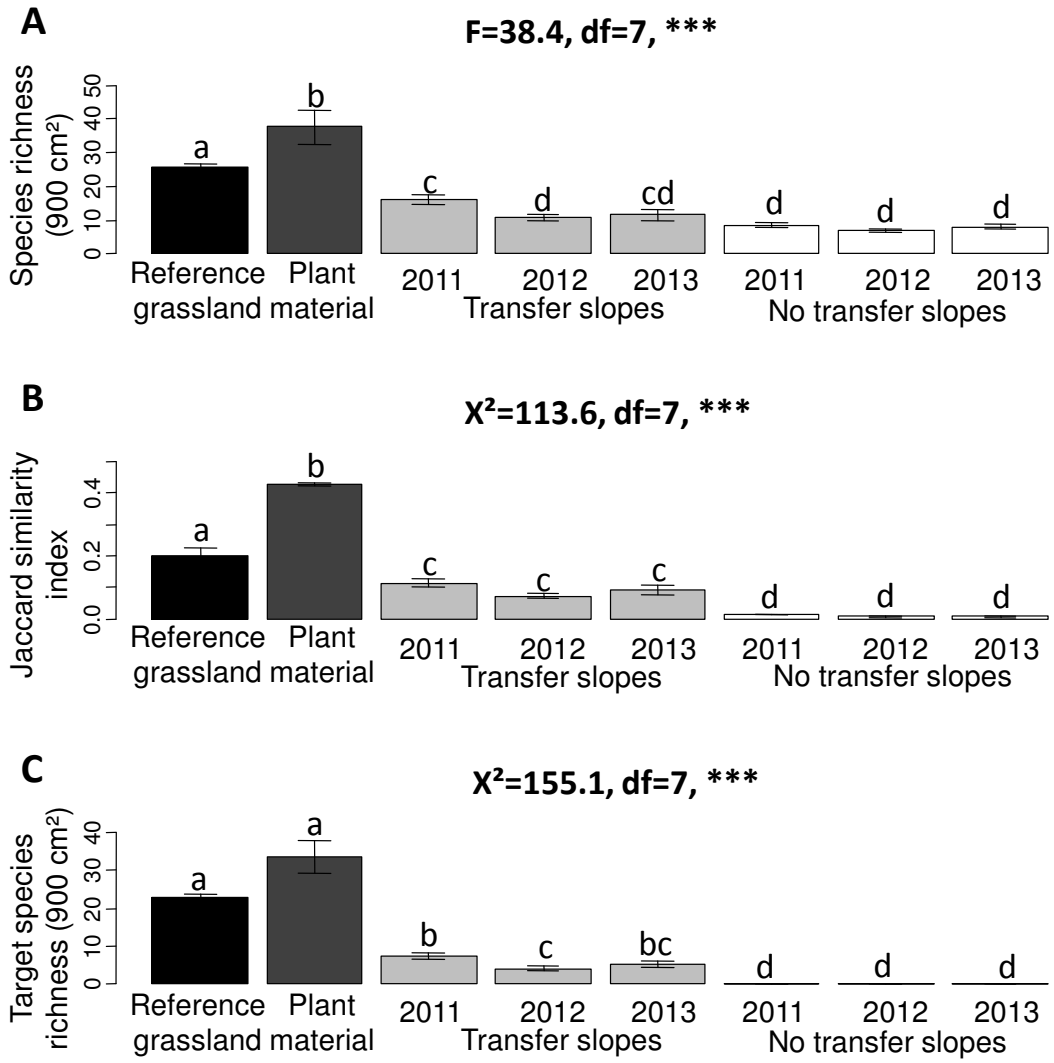

Figure 4.5: Mean and standard errors of A) species richness (900 cm²), B) Jaccard similarity index and C) target species richness (900 cm²) for the reference grassland in 2010 (black bars, n=20 plots), plant material (dark grey, n=3 plots), transfer slopes in 2011 (light grey bars, n=30 plots), transfer slopes in 2012 (light grey bars, n=30plots), transfer slopes in 2013 (light grey bars, n=30plots), no transfer slopes in 2011 (white bars, n=30 plots), no transfer slopes in 2012 (white bars, n=30 plots) and no transfer slopes in 2013 (white bars, n=30plots). Df are the degrees of freedom. The F of ANOVA or the χ^2 of Kruskal-Wallis tests performed are shown above the bars (*******: *p*<0.001), bars showing the same letters do not have any significant differences according Tukey test or to pairwise Wilcoxon multiple comparisons with Holm *p* adjustment.

4.3.4. Seed content in plant material (greenhouse)

A total of 4550 (±184) individuals representing 38 (±5) species, almost all included in the meso-xeric grassland target species category, were found in the plant material (***Appendix 2***). Plant material composition was characterized by *Brachypodium distachyon* (L.) P. Beauv. (40%), *Bromus hordeaceus* L. (23%) and *Parapholis incurva* (L.) C.E. Hubb.

(14%). The vegetation of the reference grassland was characterized by *Bellis annua* L. (8%), *Brachypodium phoenicoides* (L.) Roem. & Schult. (8%) and *Scorpiurus muricatus* L. (7%). This change in composition between the plant material and the reference grassland was revealed in the CA based on the presence of the species (**Figure 4.7**). The first axis of the CA (20.1%) did not indicate a difference in composition between the two communities, but the second axis of the CA (7.5%) discriminated the plant material from the reference grassland. These results were confirmed with the significant difference in plant species richness between the reference grassland and the plant material (37.7±5.0 for plant material *vs.* 25.7±1.1 for reference grassland; **Figure 4.5.A**). However, we found no significant difference in the number of target species (33.7±4.4 for plant material *vs.* 22.8±0.9 for reference grassland; **Figure 4.5.C**) between the reference grassland and the plant material.

4.3.5. *Effects of plant material transfer on vegetation development: comparing no transfer slopes and transfer slopes*

In the first year of monitoring, plant species richness significantly increased with plant material transfer (16.0±1.4 species and 8.5±0.9 species on the transfer slopes and the no transfer slopes respectively) but was significantly lower than the species richness of the reference grassland and of the plant material ($F=38.4$, $df=7$, $n=203$, $p<0.001$; **Figure 4.5.A**). A few months after the transfer, transfer treatment had already increased the number of target species which accounted for 46% of all the species found (7.4±0.8 target species in the transfer slopes vs. and 0.03±0.03 in the no transfer slopes) but was still lower to the ones of the reference grassland and the plant material ($\chi^2=155.1$, $df=7$, $n=203$, $p<0.001$; **Figure 4.5.C**). In the first year, the vegetation where plant material was transferred was characterized by two target species *Brachypodium distachyon* (L.) P. Beauv. (7%) and *Bromus madritensis* L. (6%) and by *Polygonum aviculare* L. (7%). However, in the second year of monitoring, the vegetation where plant material was transferred was no longer characterized by target species and was instead characterized by mesophyllous meadow species *Lolium rigidum* Gaudin (8%) and by *Polygonum aviculare* L. (5%). The plant species richness (10.8±0.9 species, $F=38.4$, $df=7$, $n=203$, $p<0.001$; **Figure 4.5.A**) and the number of target species (4.0±0.5 target species, $\chi^2=155.1$, $df=7$, $n=203$,

p<0.001; ***Figure 4.5.C***) were significantly lower compared to the first year, even when the contribution of target species to species richness was still high (37%). In the third year, the species richness (11.6±1.6) and the number of target species (5.2±1.0, with a contribution to species richness reaching 45%) in plant material transfer did not show significant differences with the second year (***Figure 4.5.A*** and ***Figure 4.5.C***) and were still characterized by mesophyllous meadow species *Trifolium repens* L. (13%) and *Poa trivialis* L. (6%). The increase in species richness in transfer slopes the first year compared to no transfer slope no longer appeared the second and the third years. No more significant difference was observed in the species richness between the second and the third years and between the two treatments (***Figure 4.5.A***). However, the Jaccard similarity index and the number of target species were significantly higher in the transfer slopes compared to those on the no transfer slopes over the three years (***Figure 4.5.B*** and ***Figure 4.5.C***). The nonparametric MANOVA showed that plant material transfer treatment modified significantly plant community compositions between transfer and no transfer slopes the three years (df=1, F=6.2, p=0.001 for the third year). The CA based on the presence of the species highlights these mixed results (a decrease in species richness over years but a higher number of target species in the transfer treatment). The first axis of the CA (20.1%, ***Figure 4.7***) discriminated the plant material and the reference grassland composition from the transfer treatment and the no transfer treatment. The transfer treatment occupied an intermediate position between the no transfer and the reference grassland/plant material grown in the greenhouse, containing both meso-xeric grassland target species and non-target species. The trajectories of their barycenter showed very slow dynamics between the first and the second year, highlighting a convergence towards the no transfer vegetation and then a higher divergence from the reference grassland, confirming that the number of target species decreased in the second year. The trajectories of their barycenter between the second and the third year suggested a convergence toward the reference grassland which may be explained by the high contribution of the target species the third year. Concerning the no transfer plot, no changes were observed in species richness and plant composition from the first to the third year (***Figure 4.5.A*** and ***Figure 4.5.B***).

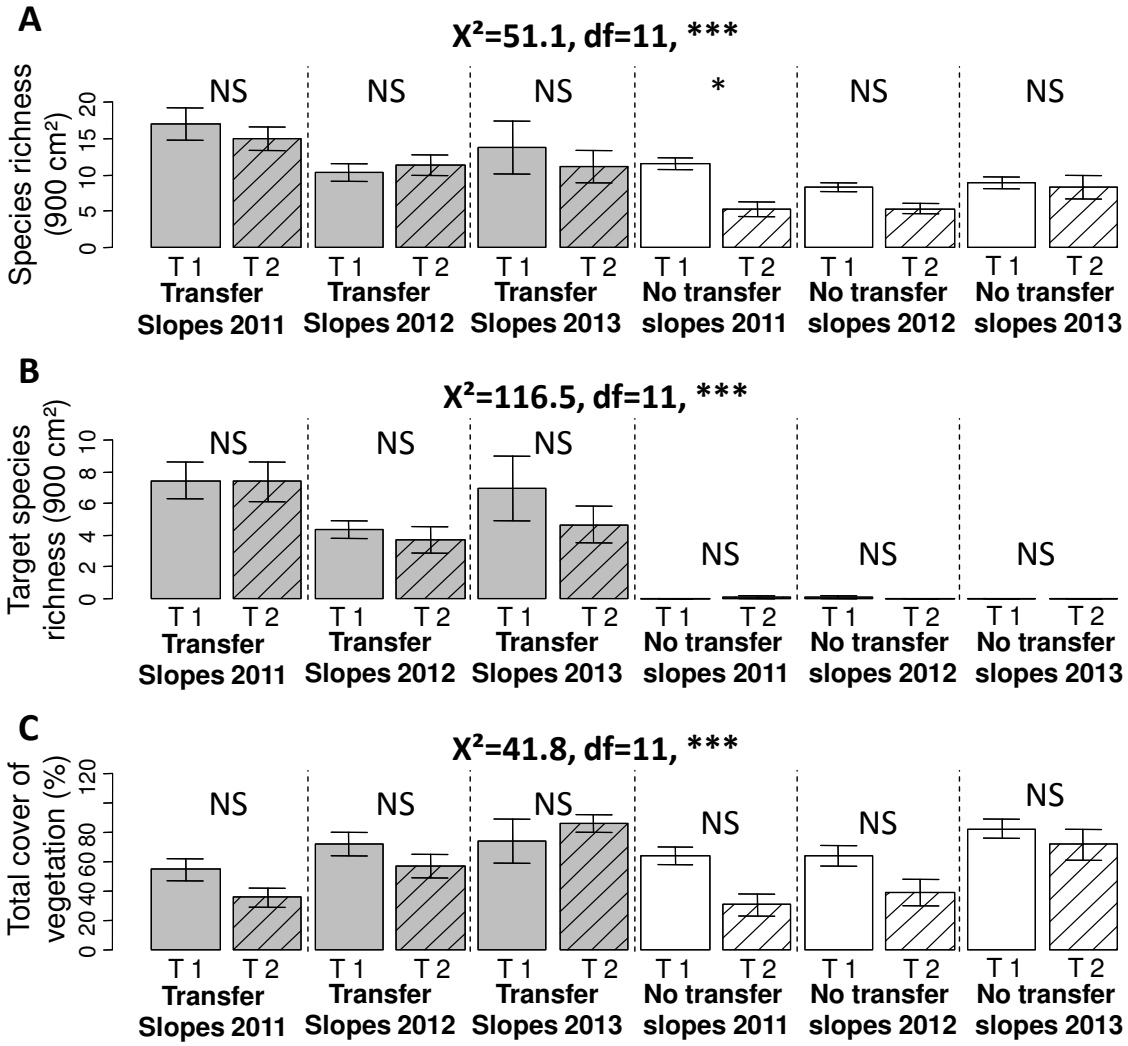

Figure 4.6: Mean and standard errors of A) species richness (900 cm²), B) target species richness (900 cm²) and C) total cover of vegetation on 900 cm² (%) for the transect 1 (T1) of transfer slopes in 2011 (grey bars, n=15 plots), in 2012 (grey bars, n=15 plots), in 2013 (grey bars, n=15 plots), for the transect 2 (T2) of transfer slopes in 2011 (shaded grey bars, n=15 plots), in 2012 (shaded grey bars, n=15 plots), in 2013 (shaded grey bars, n=15 plots), for the transect 1 (T1) of no transfer slopes in 2011 (white bars, n=15 plots), in 2012 (white bars, n=15 plots), in 2013 (white bars, n=15 plots), for the transect 2 (T2) of no transfer slopes in 2011 (shaded white bars, n=15 plots), in 2012 (shaded white bars, n=15 plots), in 2013 (shaded white bars, n=15 plots). Df are the degrees of freedom. The χ^2 of Kruskal-Wallis tests performed are shown above the bars (***: $p<0.001$). Within each treatment to compare transects, asterisks indicate significant differences according to pairwise Wilcoxon multiple comparisons with Holm p adjustment (*: $p<0.05$ and NS: $p>0.05$).

4.3.6. Effects of topsoil removal on plant material transfer: comparing transects on transfer slopes

We found no difference between the two transects in plant species richness over the three year (17.0±2.2 for transect 1 *vs.* 15.0±1.7 for transect 2 in 2011, 10.3±1.2 for transect 1

vs. 11.3±1.4 for transect 2 in 2012, and 13.8±2.3 for transect 1 *vs.* 11.2±1.4 for transect 2 in 2013; ***Figure 4.6.A***) and in the number of target species (7.5±1.1 target species for transect 1 *vs.* 7.4±1.2 for transect 2 in 2011, and 4.3±0.6 for transect 1 *vs.* 3.7±0.8 for transect 2 in 2012, and 7.0±1.3 for transect 1 *vs.* 4.7±0.7 for transect 2 in 2013; ***Figure 4.6.B***) during the three years.

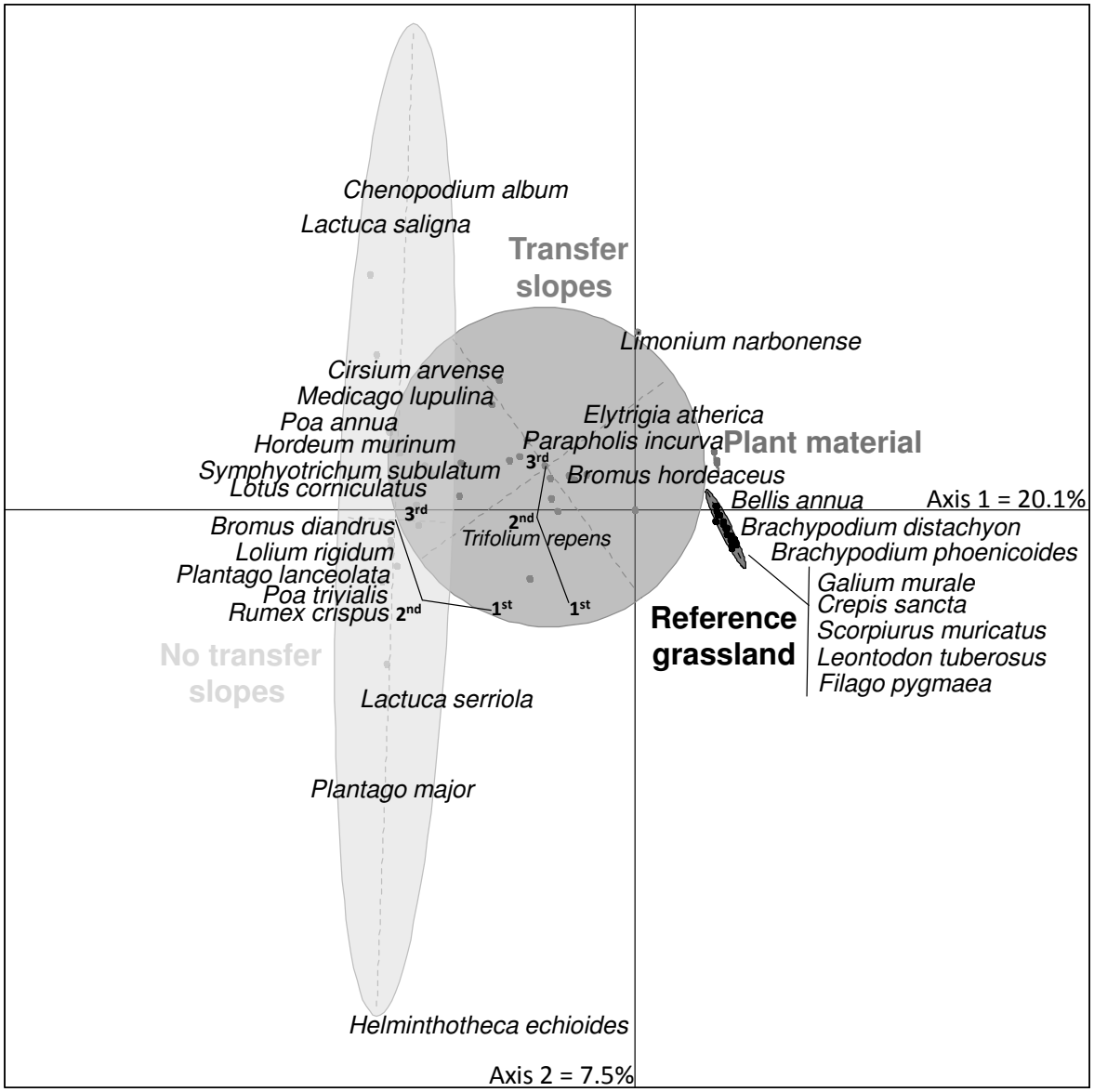

Figure 4.7: A) Ordination plot of the Correspondence Analysis based on species presence/absence of the 28 species present in at least 3 plots (83 plots × 94 species) on reference grassland (dark, 20 plots), plant material (dark grey, 3 plots), transfer slopes in 2013 (grey, 30 plots) and no transfer slopes in 2013 (light grey, 30 plots). Dark lines represent the succession of vegetation from 2011 to 2012 (1st to 2nd year), and from 2012 to 2013 (2nd to 3rd year), for transfer slope and no transfer slope, according to the position of their barycenter. In the interests of clarity, only the 50 species with the higher contributions to axis are shown.

The vegetation mean percent cover did not differ between the two transects in the first, the second, and the third years of monitoring (***Figure 4.6.C***). The MANOVA performed on the species abundances in 2013 confirmed these results and indicated no difference between the vegetation composition on transect 1 from the vegetation composition on transect 2 in transfer slopes (df=1, F=1.3, *p*=0.3).

4.4. Discussion

4.4.1. Effects of plant material transfer

The knowledge of the potential seed sources of target species in the site to-be-restored is an essential information in restoration ecology (Willems and Bik 1998). In our study site, spontaneous succession on the no transfer slopes and on-site seed bank do not indicate any potential for the establishment of target species. These results are in accordance with previous studies on former cultivation which found a low or null potential of seed banks for restoration, mainly containing ruderal seeds (Hutchings and Booth 1996; Prach et al. 2001b; Buisson et al. 2006b; Török et al. 2011a). In the present study, plant material transfer appeared to be an effective method to overcome the dispersal limitations of target species from the reference plant community. Species from transferred plant material contributed to 46% of the species richness per plot the first year of monitoring, to 37% the second year and to 45% the third year. This transfer rate is in the range of what has already been observed in previous plant material transfer studies (e.g. 64% the first year of transfer and 49% four years after the transfer in (Hölzel and Otte 2003). However, this relative high contribution of target species the third year, also corresponded to a significant decreasing of the species richness and the number of target species between the first and the second years and a stabilization between the second to the third year. This decrease led to the lack of difference in the species richness with the no transfer slopes over the years. This type of decrease has been reported in a few studies, showing that both the similarity with the reference community and the species richness declined after a few years (Pywell et al. 2007; Klimkowska et al. 2010b). Nevertheless, most studies on transfer experiments, found that the number of target species increased along with species richness whereas non-target species, such as

pioneer species or arable weeds, dominating the vegetation immediately after the plant materiel transfer, declined the following years (Kirmer and Mahn 2001; Hölzel and Otte 2003; Kiehl and Wagner 2006; Donath et al. 2007; Rasran et al. 2007; Coiffait-Gombault et al. 2011). Those studies suggested that the initial phase of succession does not determine the final community, and that, despite competition, transfer may limit the recruitment of non-target species from the seed bank by establishing a target vegetation. In our study, despite the decrease in the number of target species, one new target species appeared the second year (*Hedypnois cretica* (L.) Dum.Cours.) and another new one the third year (*Torilis nodosa* (L.) Gaertn.).This weak second phase of recruitment might be explained by the fact that some species present in the plant material require specific conditions to germinate or develop much slower. In previous plant material experiments (Hölzel and Otte 2003; Donath et al. 2007), some target species first appeared several years after the transfer, indicating a longer seed dormancy or hard-to-meet germination conditions. Obviously, germination conditions in the greenhouse (favorable temperature and water regime, lack of competition) allowed the expression of many more seeds and species than in the field.

The decrease in species between 2011 and 2012 might be also explained by differences in weather conditions between the two years. Indeed, drought can reduce species richness in grassland communities (De Boeck et al. 2008). In contrast, Török et al. (Török et al. 2012) indicated that high precipitation might have altered the competitive environment favoring the establishment of some target species. However, our vegetation monitoring in the reference grassland and in the no transfer treatment, did not show a decrease in species richness between 2011 and 2012 (***Figure 4.3.B***), indicating that the decrease was probably not due to differences in weather conditions.

The decrease might also partially be caused by the increase in competition and the influence of local processes (Kiehl and Wagner 2006; Klimkowska et al. 2010b). Seed limitation is not always the only limiting factor in species establishment (Turnbull et al. 2000; Mouquet et al. 2004; Clark et al. 2007; Myers and Harms 2009); the successful establishment of many plant species depends on more than simply germination conditions. Other factors, in particular competition, can influence community assembly. Non-target species, such as mesophyllous meadow or ruderal species resident in the

Cassaïre site and in the seed bank, can have a negative effect on the germination and growth of target species transferred with the plant material, because the latter are less competitive. This decrease can be partially explained by the inadequate timing of the management: mowing was only performed quite late following the plant material transfer (one full calendar year later). Moreover, grazing has several advantages for grassland restoration compared to mowing (Török et al. 2011b) and the Mediterranean meso-xeric grasslands in the Camargue area are managed by traditional extensive on-and-off livestock grazing throughout the year for conservation purposes, maintaining open habitats (Peco et al. 1998). Grazing management similar to that applied on the reference grassland is required. By controlling competition, plant biomass removal by grazing can increase species richness and change the competitive interactions in favor of smaller, stress-tolerant species (Lepš 1999; Bakker et al. 2006; Pywell et al. 2007; Rasran et al. 2007; Myers and Harms 2009). Grazing is known to be an efficient tool in maintaining a grassland community (Hölzel and Otte 2003; Walker and Desanker 2004; Rasran et al. 2007; Klimkowska et al. 2010b). It can reduce the abundance of ruderal, competitive, and mesophyllous meadow species, which leads to an increase in the abundance of rare species (Woodcock et al. 2005). It also creates, through trampling, micro-sites which increase recruitment opportunities for immigrating species (Bakker et al. 2006; Myers and Harms 2009). Although the percentage of target species remained stable in the vegetation over the third year of monitoring, the initial decrease in species richness suggests a future dominance of competitive species, which may form dense compact cover rarely outcompeted by other species, and may lead to the disappearance of target species without appropriate management. In this study, we deliberately introduced mowing late after the plant material transfer, to allow target vegetation to establish and not to disturb the reproductive cycle of some of these species which are annual. Indeed, grazing and mowing could have hampered restoration and negatively affected the target vegetation (Török et al. 2011b). The timing of grazing/mowing is crucial in influencing the success of restoration and appears as a compromise between the establishment of target species and the control of the non-target species. By delaying the management, we probably facilitated the competition of the non-target species of the soil seed bank.

4.4.2. Effects of topsoil removal

The success of plant material transfer usually increases when it is applied in conjunction with topsoil removal which creates favorable conditions for seedling recruitment. It limits the proportion of unwanted plant species, such as arable weeds and common meadow species and then favors the establishment of target species (Patzelt et al. 2001; Hölzel and Otte 2003; Kiehl and Wagner 2006; Pywell et al. 2007; Klimkowska et al. 2010b; Jaunatre et al. 2012). Topsoil removal generally also leads to a reduction in non-target species by reducing the seed bank and limiting the immediate reinvasion and colonization by non-target plants from the seed bank. The resulting presence of bare soil allows for the establishment and maintenance of the oligotrophic target community (Patzelt et al. 2001; Allison and Ausden 2004; Kiehl et al. 2010). A clear example of the importance of these factors can be found in abandoned cultivation sites, where the seed bank can indirectly control the establishment of target species because of the abundance of competitive or ruderal species (Lepš 1999; Hölzel and Otte 2003; Kiehl and Wagner 2006; Pywell et al. 2007; Standish et al. 2008; Baer et al. 2009). In our case, we found no significant difference on the number of seedlings and the species richness in the seed bank between 5 cm and 20 cm. This vertical homogenization of the seed bank can be explained by the technical rice cultivation practices, which included a 20 cm deep plowing. In Hölzel & Otte (2003), soil seed bank was completely eliminated at 50 cm deep in a former arable field. In most studies, the removal of the upper 30-50 cm ensures favorable conditions for restoration (Rasran et al. 2007; Klimkowska et al. 2010b; Török et al. 2011b). However, a topsoil removal at such depth can be too expensive to be used on large areas.

On our study site, the initial hypothesis of a decrease in vegetation cover, of a limitation of the competition and of an increase in the plant material transfer efficiency with increasing depth of topsoil removal was not confirmed, because of the lack of an appreciable difference in soil seed bank between 5 cm and 20 cm. Differing from our results, Klimkowska et al. (2010b) found that vegetation in the deep removal treatment with hay addition were more similar to the reference vegetation that shallow removal treatment with hay.

Forty cm depth topsoil removal resulted in a significant reduction of P2O5, organic matter, total C and total N. Topsoil removal therefore decreased the nutrient content, which is in agreement with similar experiments (Aerts et al. 1995; Patzelt et al. 2001; Tallowin and Smith 2001; Hölzel and Otte 2003; Allison and Ausden 2004; Buisson et al. 2006b; Buisson et al. 2008; Kiehl et al. 2010; Jaunatre et al. 2012). Cultivation practices induce severe constraints on community re-assembly (Gough and Marrs 1990; Pywell et al. 2003) and despite seed addition, species of oligotrophic grasslands establish poorly in excessively high-fertility conditions (Pywell et al. 2003) as they require nutrient-poor site conditions to establish themselves successfully (Temperton et al. 2012). Topsoil removal appears to be an efficient method of improving the environmental conditions while mitigating competition by reducing seed bank for reinstalling meso-xeric grasslands on abandoned farmland.

Three years after the application of the combination of the two treatments, the restored plant communities are still very different from our target community. However, these restoration treatments increased the number of target species and enhanced the similarity to the reference grassland. They might help to bypass some of the early stages of natural succession. Over the three years, the vegetation cover increased (from 35% to 86%; ***Figure 4.6.C***) potentially slowing the spontaneous recruitment of target species. The introduction of target species in the early stages of succession allowed their presence in the community. This presence could play a major role in the development of community. Indeed, some restoration projects have already tested the priority effect of target species (foundation or structural species) in grasslands (Coiffait-Gombault et al. 2012) or wetlands (Collinge and Ray 2009). In our study, *Brachypodium distachyon* (L.) P. Beauv. which is common on the reference grassland, abundantly appeared the first year of monitoring in the transfer treatment, and could thus be a key species which help to improve restoration by accelerating the achievement to the full target community.

Our study showed that some meso-xeric grassland target species can be reintroduced on a former ricefield by a combination of low topsoil removal and plant material transfer. This is in accordance with other studies (Patzelt et al. 2001; Hölzel and Otte 2003; Kiehl and Wagner 2006; Rasran et al. 2007; Klimkowska et al. 2010b) demonstrating that these two methods are complementary, involving different processes

of community assembly: plant material transfer overcomes the dispersion filter and topsoil removal guarantees better abiotic and biotic conditions.

Although most studies on topsoil removal have shown that deeper topsoil removal is more appropriate for target species establishment (Hölzel and Otte 2003; Rasran et al. 2007; Klimkowska et al. 2010b), our study does not discriminate the two different topsoil removal depths in term of soil seed banks (species richness and number of seedlings), resulting in lack of difference for species richness and target species number between the two topsoil removal depth. Taking in account the high cost of this method (Klimkowska et al. 2010a), we suggest to look the seed bank before choosing the thickness of topsoil to remove as in our case, 5 cm were sufficient to eliminate half of the undesired seed bank. However without seed addition, spontaneous succession did not provide successful results. Plant material plays an important role in the early community assembly processes and speeds up the establishment of target species. Harvesting at different times during all the flowering period and with different methods (mowing and vacuuming) allowed us to have a good plant material quality (Stevenson et al. 1995), maximizing the number of target species, containing the early and the late flowering species, with a composition closer to that of the donor site. In order to do restoration on large area, plant material may be collected by harvesting machines (Kiehl et al. 2010). The densities used in our pilot experiment corresponds to 150 kg of material per hectare, which is a much higher quantity than in most plant material transfer studies (Török et al. 2011b). In order to limit the quantity of material and thus reducing the harvest effort, the relevancy to transfer plant material by only small patches, functioning as species-rich sources for spontaneous colonization of nearby areas, might be used (Rasran et al. 2007; Török et al. 2011b). This method is currently tested on the Cassaïre site especially to evaluate the consequences of the existence of patches without material spread which could be, a contrario, windows of colonization for undesirable species.

To be effective at restoring large scale Mediterranean meso-xeric grassland, plant material transfers must therefore be combined with an appropriate grazing management. Grazing has played a major role in the reference grassland structuring the plant community over time, and is probably essential to maintain a good trajectory to obtain on the site in current restoration the desired vegetation in the mid-or long term.

Transition to Discussion

Chapter 3 and ***Chapter 4*** assessed techniques for meso-xeric grassland and temporary wetland restoration in small-scale experiments. They showed some positive effects on the two ecosystems even it is more obvious for the temporary wetland. In April 2012, several complementary experiments were carried out on a large scale in order to assess the efficiency of these techniques at the ecosystem scale. Restoration techniques were adapted to the operational scale to try to mitigate the costs of restoration without affecting restoration success: the density of plant material transfer and the area of inoculation (i.e. introduction design) were tested in large scale. The large scale experiments were monitored in June 2012, but were not presented in this thesis. Nevertheless, we can provide a summary of preliminary results concerning i) the transfer of restoration techniques tested and approved in ***Chapter 3*** and ***Chapter 4*** to the operational scale, ii) the effect of various plant material density for grassland community, iii) the effect of area of inoculation and iv) the potential priority effects detected on this scale for the grassland community.

TD.1. Effect of introduction design on the temporary wetland

The same soil used in the block experiments (***Chapter 3***) was inoculated on plots of 6 m × 6 m according to the following four treatments (***Figure TD.1***): inoculated on 100% of the area (72 liters of soil inoculated in the whole plot), inoculated on 1/3 of the area on two strips (36 liters of soil spread over two 1-m wide and 6-m long strips , spaced by 1.5 m from the edge of the plot and by 1 m between each other), inoculated on 1/3 of the area on one strip (36 liters of soil spread over one 2-m wide and 6-m long strip, 2 m from the edge of the plot) and control (not inoculation) with five replicates per treatment. The twenty plots were disposed randomly to the 4000m² restored area. The inoculation was done in April 2012.

Vegetation surveys were carried out using nine 2 m × 2 m quadrats in June 2012 (2 months after soil inoculation) and May 2013 (13 months after soil inoculation), covering the whole plots, recording the presence/absence of all species, and an average of the species richness on the nine quadrats was calculated.

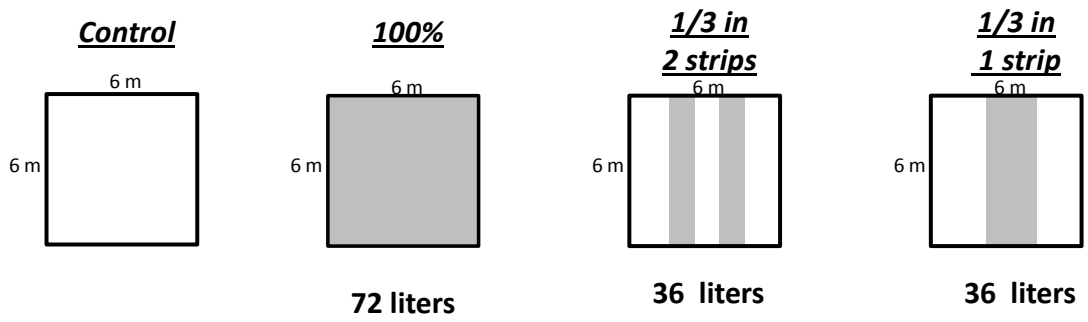

Figure TD.1 : The four experimental introduction design tested in large scale for the temporary wetland. The grey shading indicates the soil inoculation in the plots.

Plant species richness (***Figure TD.2.A***) and target species richness (***Figure TD.2.B***) significantly increased with soil transfer relative to the control, but no difference were observed between various types of inoculation. Results are discussed in ***Discussion***.

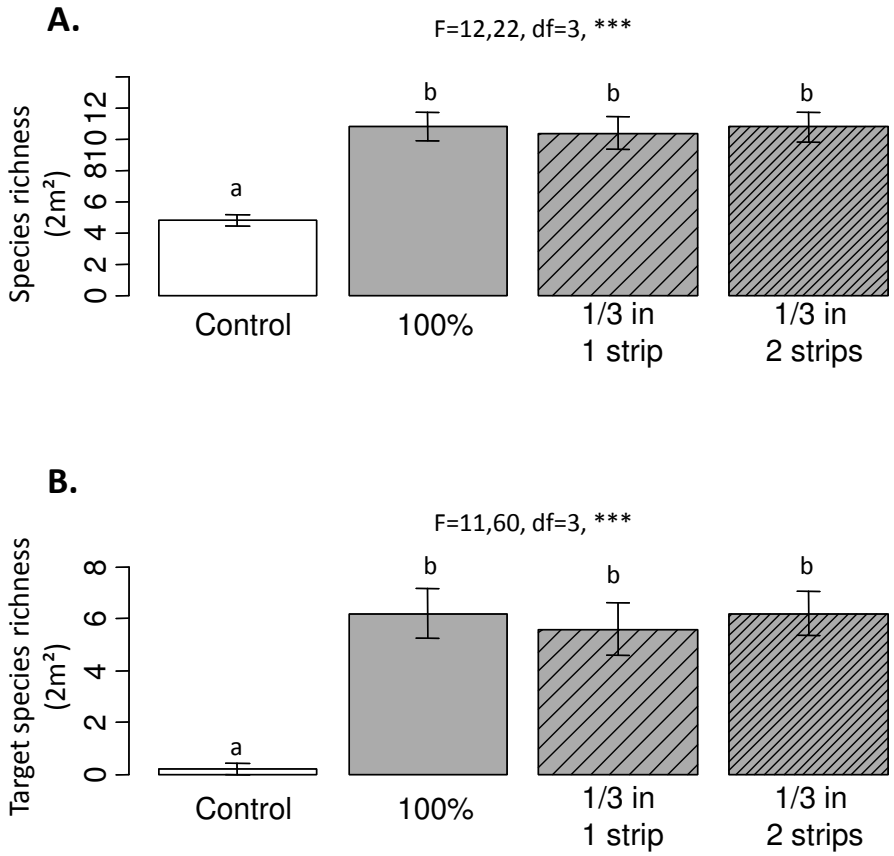

Figure TD.2 : Mean and standard errors of species richness (A) and target species number (B) for control (white bars, n=5 plots), 100% soil inoculation (grey bars, n= 5 plots), 1/3 inoculate in 1 strip (large shaded grey bars, n= 5 plots) and 1/3 inoculate in 2 strips (tight shaded grey bars, n= 5 plots). The F of ANOVA tests are shown above the bars (*** : $p<0.001$), different letters above bars indicate significant differences according to Tukey post-hoc tests.

TD.2. Effect of introduction design and density on the meso-xeric grassland

In addition to the experimental introduction design, two plant material densities were tested, a high density (DF = 43.4g / m²) and low density (df = DF / 2 = 21.7g / m²). The same plant material as the one used in the block experiments (***Chapter 4***) was inoculated on plots of 3 m × 3 m according to the following seven treatments (***Figure TD.3***): inoculated on 100% of the area (196 g of plant material inoculated on the whole plot), inoculated on half of the area in two strips (98 g of plant material over two 0.75-m wide and 3-m long strips, spaced by 0.5 m from the edges of the plot and by 0.5 m between each other), inoculated on half of the area on one strip (98 g of plant material over one 1.5-m wide and 3-m long strip, 0.75 m from the plot edges) at low density and inoculated on 100% of the area (391 g on the whole plot), inoculated on half of the area in two strips (196 g over two 0.75-m wide and 3-m long strips, spaced by 0.5 m from the plot edges and by 0.5 m between each other), inoculated on half of the area on one strip (196 g over one 1.5-m wide and 3-m long strip, 0.75 m from plot edges) in high density and control, with four replicates per treatment. The twenty eight plots were disposed randomly to the 3000m² restored area. The inoculation was carried out in April 2012.

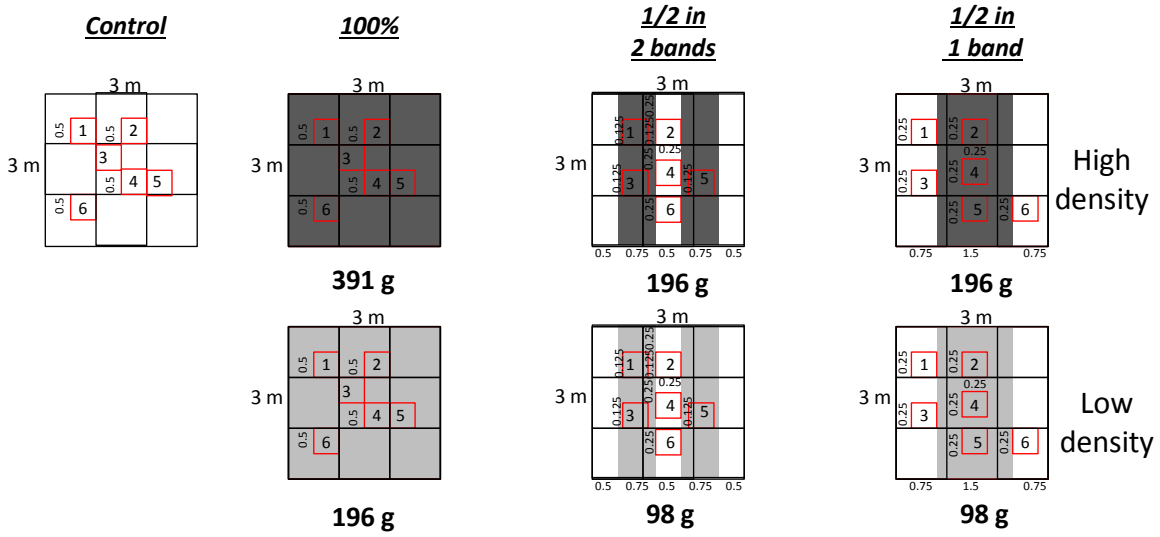

Figure TD.3 : The seven treatments tested at the operational scale for grassland. The grey shading indicates the plant material inoculation in the plots (dark grey: high density ; light grey: low density). The red squares indicate the permanent quadrats used to survey vegetation.

Vegetation surveys were carried out using six permanent 0.5 m × 0.5 m quadrats (***Figure TD.3***) in June 2012 (2 months after inoculation of plant material) and May 2013 (13

months after inoculation of plant material), recording the presence/absence of all species using the same method that in the block experiments, and an average of species richness of the six quadrats was calculated.

Plant species richness (***Figure TD.4.A***) and target species richness (***Figure TD.4.B***) significantly increased with plant material transfer relative to the control, but no difference were observed between various types of inoculation and the density two months after the introduction. Results are discussed in ***Discussion***.

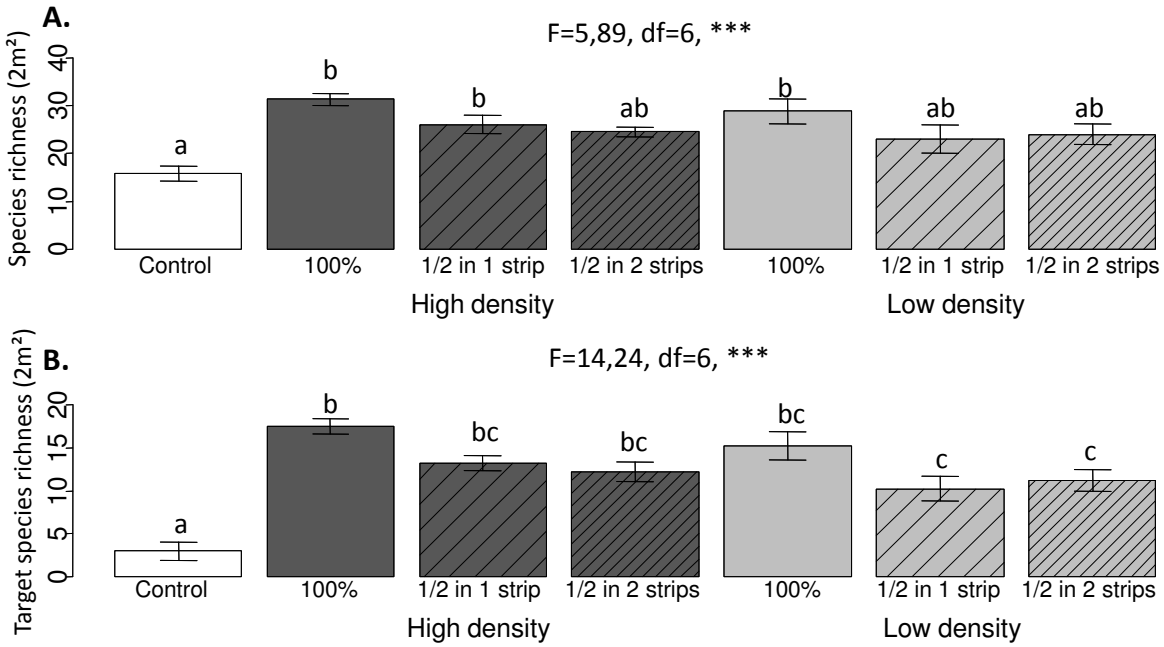

Figure TD.4 **:** Mean and standard errors of species richness (A) and target species number (B) for control (white bars, n=4 plots), 100% plant material inoculation (dark grey bars, n= 4 plots), 1/2 inoculate in 1 strip (large shaded dark grey bars, n= 4 plots) and 1/2 inoculate in 2 strips(tight shaded dark grey bars, n= 4 plots) in high density and 100% soil inoculation (light grey bars, n= 4 plots), 1/2 inoculate in 1 strip (large shaded light grey bars, n= 4 plots) and 1/2 inoculate in 2 strips (tight shaded light grey bars, n= 4 plots) in low density in June 2012. The F of ANOVA test are shown above the bars (******* : $p<0.001$), different letters above bars indicate significant differences according to Tukey post-hoc tests.

TD.3. Improvement of diversity in restoration experiment with keystone species

These preliminary results on the potential priority effects were established from field observations on the large scale grassland restoration, where some targets species, according to their structure and biomass, seemed to aggregate the other species transferred with the plant material.

Using the inoculated quadrats, we calculated for each target species the species richness (global and in target species) in each quadrat with and without the target species, to see any effect of this species on global species richness and on target species richness.

Out of the 36 target species, 13 showed significant increase in species richness and in the number of target species with their presence. If for some of those species, this correlation just indicated a site effect (increase in the species richness because the site is favorable to an increase in species), for three species (***Figure TD.5***), where an aggregation was showed in the field during the vegetation surveys, this correlation can indicated a facilitation effect and may provide priority effect. The monitoring used here is not efficient to bring out this biotic interactions effect. The results and some research perspectives are discussed in ***Discussion***.

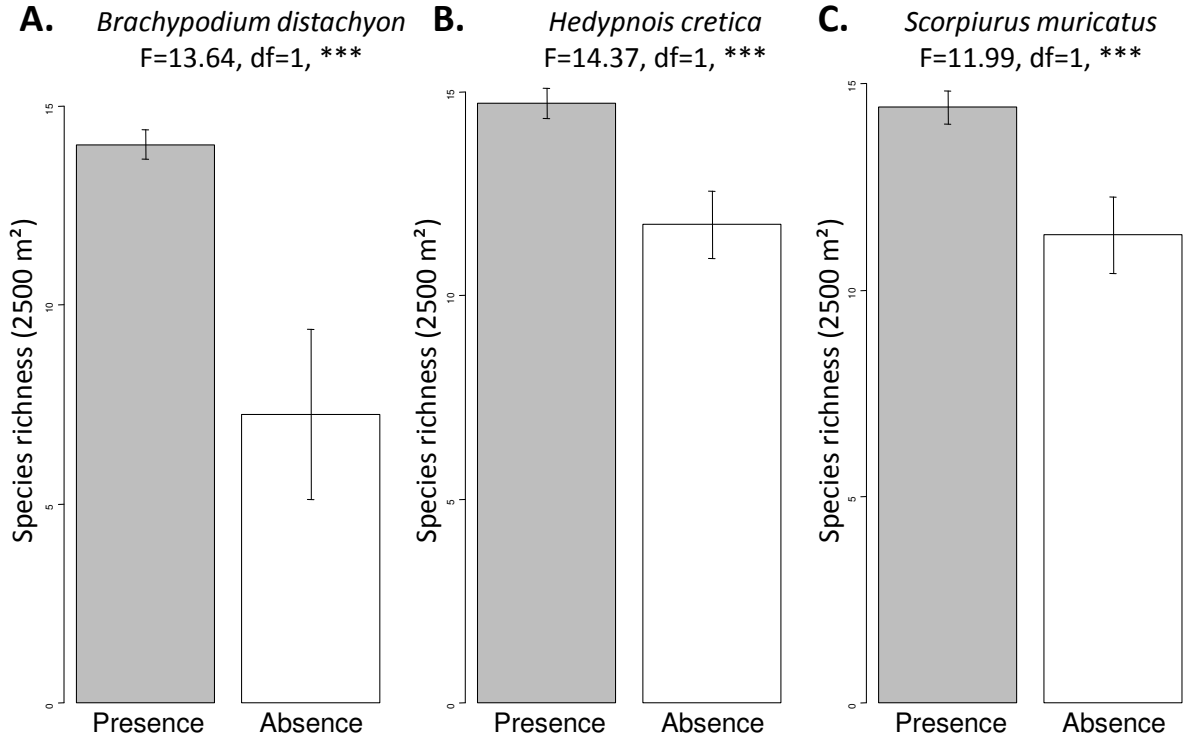

Figure TD.5 **:** Mean and standars errors of species richness with the presence (grey bars) or with the absence (white bars) of *Brachypodium distachyon* (A), *Hedypnois cretica* (B) and *Scorpiurus muricatus* (C). The F of ANOVA test are shown above the bars (******* : p<0.001), different letters above bars indicate significant differences according to Tukey post-hoc tests. Same results were observed with the number of target species in the absence or the presence of these three species.

The Cassaïre site creation at large scale using a bulldozer to create topography.

Aerial photography of the Cassaïre site during the creation (foreground the arable field, in background the wetland of the National Nature Reserve Les Marais du Vigueirat).

Discussion Générale

La thèse a pour objet la création de marais temporaires méditerranéens et de pelouses méso-xériques méditerranéennes sur d'anciennes rizières (***Figure D.1***).

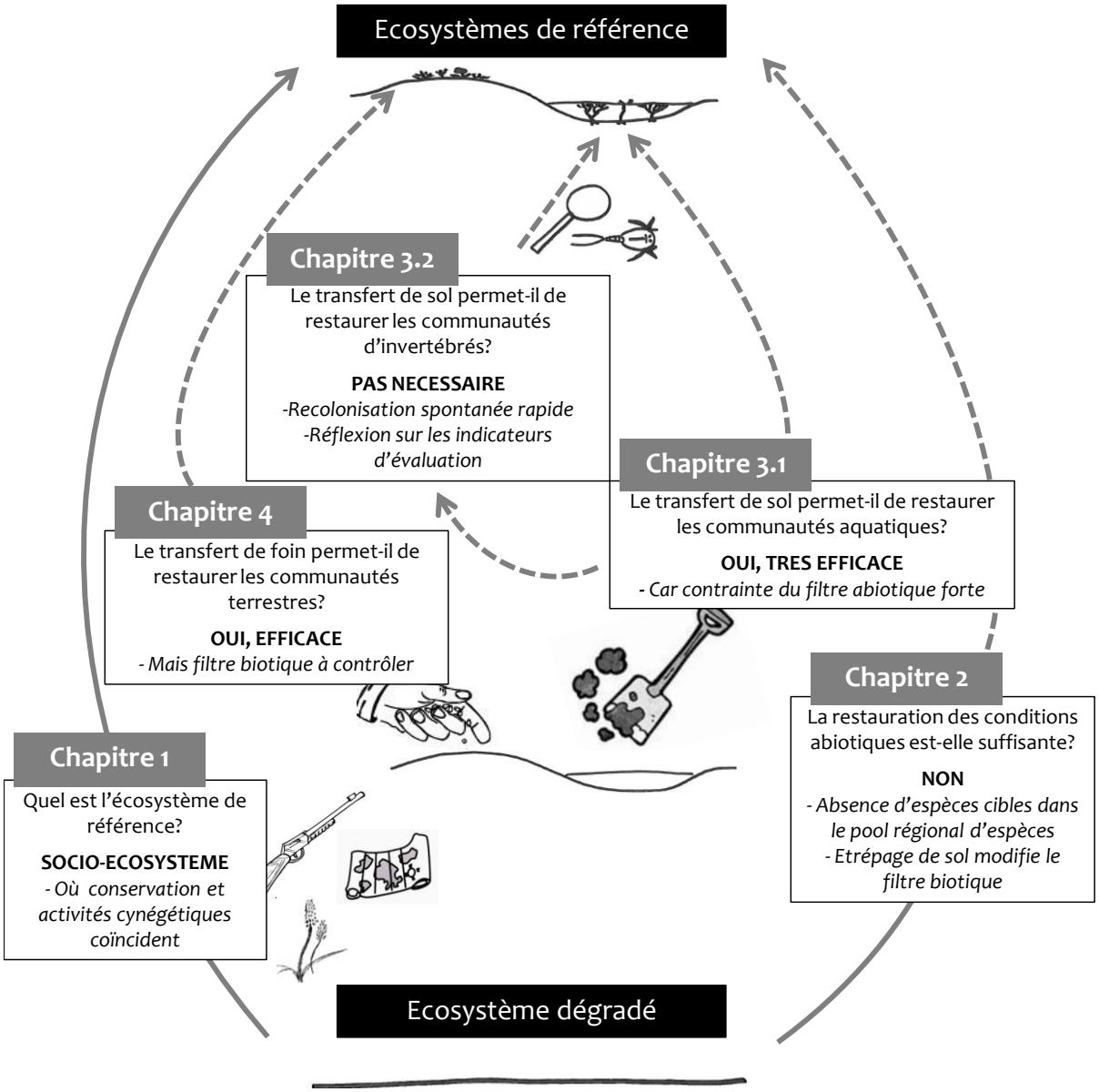

Figure D.1 **:** Schéma général d'organisation de thèse et principaux résultats acquis.

Les choix effectués concernant les écosystèmes de référence et leur justification sont l'objet du ***chapitre 1***. La restauration des conditions abiotiques seule ne permet pas un changement de trajectoire des communautés végétales dans les directions escomptées, en raison notamment de l'absence de graines d'espèces cibles dans le pool régional d'espèces (***chapitre 2***). Dans un tel contexte, la manipulation de la dispersion par le transfert de graines d'espèces cibles est donc nécessaire. Pour les communautés

végétales des marais temporaires, le transfert de sol après restauration des conditions abiotiques semble permettre l'expression de la totalité des espèces végétales transférées, une augmentation de la similarité avec la communauté de référence et une diminution des espèces identifiées comme indésirables (***chapitre 3.1***). Cette technique apparaît moins pertinente pour les communautés d'invertébrés aquatiques, probablement en raison de leur plus grande capacité à coloniser un milieu sans qu'il soit nécessaire de procéder à des introductions (***chapitre 3.2***). Le succès contrasté de l'inoculation de sol, en fonction du compartiment observé (plantes ou invertébrés), souligne les risques à ne privilégier qu'un nombre restreint d'indicateurs de restauration, qui ne reflètent pas nécessairement l'ensemble de l'écosystème. L'étrépage de sol (i.e. qui permet de rendre les conditions abiotiques plus favorables) suivi d'un transfert de foin apparaît être une combinaison pertinente pour recréer des communautés végétales de pelouses méso-xériques méditerranéenne (***chapitre 4***).

D.1. Connaissances acquises en écologie des communautés et en écologie de la restauration

D.1.1. Les mécanismes déterminant les communautés végétales

Le modèle des filtres présenté en ***Introduction section I.4.4*** fournit un cadre théorique pour la compréhension de l'assemblage des communautés végétales (Keddy 1992; Fattorini and Halle 2004; Lortie et al. 2004; Guisan and Rahbek 2011). L'étude des mécanismes successionnels par le prisme des filtres peut également être un outil pour le pilotage des communautés végétales. A travers les différents chapitres de ce manuscrit, nous avons ainsi cherché à évaluer l'importance respective des filtres (i.e. dispersion, abiotique et biotique) dans l'installation des communautés végétales. Compte tenu de la difficulté de caractériser précisément toutes les composantes abiotiques d'un écosystème (Miller and Hobbs 2007), la restauration des conditions abiotiques n'est bien évidemment, dans notre étude, qu'une amélioration de certaines conditions abiotiques identifiées importantes dans l'assemblage de ces communautés (i.e. diminution des teneurs en nutriments du sol pour les pelouses meso-xériques et établissement du régime hydrique pour les marais temporaires). Cette restauration des conditions biotiques est

une démarche nécessaire dans un projet de restauration pour espérer atteindre les communautés de référence (***chapitre 2***, Galatowitsch and Valk 1996; Lepš 1999; Prach et al. 2001b; Bischoff 2002; Hobbs and Norton 2004; Kiehl et al. 2010; Bornette and Puijalon 2011), elle n'est cependant pas suffisante. La présence d'un pool régional d'espèces présentant des espèces des communautés cibles est également déterminante. L'absence d'espèces cibles dans la pluie de graines, la banque de graines et/ou la végétation exprimée, constatée dans notre étude suggère que la restauration des conditions abiotiques ne suffit pas à elle seule mais qu'une introduction de propagules soit au moins nécessaire pour obtenir les espèces cibles rapidement. La succession spontanée après restauration des conditions abiotiques a ici été étudiée sur une courte durée (***chapitre 2***); elle ne permet pas de mettre en évidence l'importance de mécanismes se déroulant sur des pas de temps plus long tels que la zoochorie, connue pour jouer un rôle important dans la recolonisation spontanée (e.g. pour la dispersion des espèces des marais temporaires par les oiseaux d'eau (Figuerola and Green 2002a; Brochet et al. 2010a); pour la dispersion des espèces des pelouses par le bétail (Stevens 1932; Fischer et al. 1996)). A plus long terme, une recolonisation spontanée par les espèces cibles est possible, cependant manipuler le filtre de la dispersion en introduisant des espèces cibles en début de succession végétale peut permettre (i) d'éviter des phases de blocage par des espèces non désirées présentes dans le pool régional d'espèces par des mécanismes de préemption (Reinartz and Warne 1993; Prach et al. 2001a; Prach et al. 2001b; McKinstry and Anderson 2005; Collinge and Ray 2009) et (ii) d'augmenter l'imperméabilité à des événements stochastiques (i.e. recrutement d'espèces non désirées) qui peuvent également limiter l'établissement ou le développement spontanée de nos espèces cibles (Van der Putten et al. 2000). Dans notre cas, le fait de manipuler les filtres des conditions abiotiques et de la dispersion ne permet pas pour autant d'accéder directement aux communautés végétales visées (***chapitre 3.1*** et ***chapitre 4***). Alors que des graines d'espèces cibles sont présentes et que les conditions abiotiques sont restaurées, l'absence de l'installation complète de nos communautés cibles (particulièrement dans le cas des communautés terrestres, voir section ***Discussion section D.2.1***), suggère un rôle important des interactions biotiques. En l'absence d'intervention (e.g. coupe, pâturage) ces interactions biotiques semblent menacer la reproduction et le maintien des espèces

cibles présentes et donc hypothéquer à terme la restauration des communautés (Baer et al. 2009; Jaunatre et al. 2012). Pour être efficace, le forçage de la dispersion doit être accompagné du contrôle de la compétition des espèces non désirées, dont la forte présence sur le site est liée à une forte disponibilité en nutriments, résultante des intrants des activités agricoles passées (Gough and Marrs 1990). Utilisés comme régimes de perturbation, le pâturage des pelouses méso-xériques et l'assec estival des marais temporaires, sembleraient efficace pour contrôler ces interactions biotiques défavorables à la restauration de nos communautés de référence. En limitant la biomasse, en réduisant l'abondance des espèces rudérales et mésophiles et en créant par le piétinement des micro-sites facilitant le recrutement, le pâturage permet habituellement de diminuer la compétition et favoriser ainsi l'installation de nos communautés végétales cibles (Hölzel and Otte 2003; Walker and Desanker 2004; Woodcock et al. 2005; Bakker et al. 2006; Pywell et al. 2007; Rasran et al. 2007; Myers and Harms 2009; Klimkowska et al. 2010b; Coiffait-Gombault et al. 2011; Török et al. 2011a). En sélectionnant des espèces adaptées au caractère temporaire (i.e. les espèces cibles), en défavorisant les espèces non adaptées (i.e. espèces terrestres ou espèces aquatiques à inondation estivale favorisée par la riziculture) l'assec estival limite les interactions biotiques. Soumettre nos deux communautés de référence à ces perturbations ne parait cependant pas l'unique moyen d'éviter la compétition. En effet, *via* le forçage de la dispersion et la restauration des conditions abiotiques, les interactions biotiques défavorables peuvent indirectement être réduites.

L'introduction de matériel végétal (i.e. transfert de foin et transfert de sol) contrecarre le filtre de la dispersion mais est également susceptible de modifier les interactions biotiques. En effet, le transfert de foin/sol, en augmentant la densité du couvert végétal (mis en évidence pour le transfert de sol pour les communautés aquatiques dans le ***chapitre 3.1*** mais non mis en évidence dans le transfert de foin pour les communautés terrestres dans le ***chapitre 4***) freine l'expression de la banque de graines et des espèces non désirées (Van der Putten et al. 2000; Klimkowska et al. 2010b; Török et al. 2011a; Török et al. 2012; ***chapitre 3.1***). Divers auteurs ont cependant montré qu'un couvert végétal trop dense, dû au transfert de matériel végétal, était, *a contrario*, susceptible de freiner le recrutement et l'établissement ultérieurs d'espèces cibles

(Jongepierová et al. 2007; Lepš et al. 2007; Ruprecht et al. 2010; Török et al. 2010; Török et al. 2011a). Dans notre cas, la diminution de nos espèces cibles dans les communautés de pelouses restaurées peut être en partie attribuée à l'absence de gestion appropriée de la compétition par les espèces non désirées présentes sur le site (***chapitre 4***).

L'étrépage de sol, utilisé pour rendre les conditions abiotiques plus favorables à nos espèces cibles (i.e. diminution des quantités de nutriments dans le sol) modifie également les interactions entre espèces en éliminant une partie de la végétation et de la banque de graines (mis en évidence dans le ***chapitre 2***), limitant ainsi l'installation des espèces non désirées et potentiellement compétitrices (Aerts et al. 1995; Patzelt et al. 2001; Tallowin and Smith 2001; Hölzel and Otte 2003; Allison and Ausden 2004; Buisson et al. 2006b; Buisson et al. 2008; Kiehl et al. 2010; Klimkowska et al. 2010b; Török et al. 2011b; Jaunatre et al. 2013a). Une forte teneur en nutriments n'empêche pas nécessairement les espèces cibles de s'installer, mais compromet leur persistance par la présence d'espèces non désirées (directement liée aux conditions environnementales) et les interactions négatives qui en découlent (Yurkonis and Meiners 2004; Buisson et al. 2006b).

Les filtres sont pour partie dépendants les uns des autres et la manipulation d'un filtre peut modifier indirectement un autre filtre (***Figure D.2***). Afin de lutter contre la compétition par des espèces non désirées il convient d'agir dès le début de processus de restauration. En effet, le transfert des espèces cibles sur un sol nu améliore fortement la probabilité de succès du transfert, les interactions biotiques étant faibles ou nulles (Kiehl et al. 2010), ce qui n'est pas le cas ultérieurement, les processus internes à la communauté jouant un rôle de plus en plus important (Sutherland 1974; Turnbull et al. 2000; Klimkowska et al. 2010b).

Certaines espèces cibles via des interactions positives peuvent modifier la composition de la communauté dans une direction souhaitée (***Transition to Discussion section TD.3***). L'ordre d'arrivée des espèces, qui est un processus largement stochastique et qui peut être manipulé en restauration écologique, est ainsi un mécanisme important pour la structuration ultérieure de la communauté (Fukami et al. 2005).

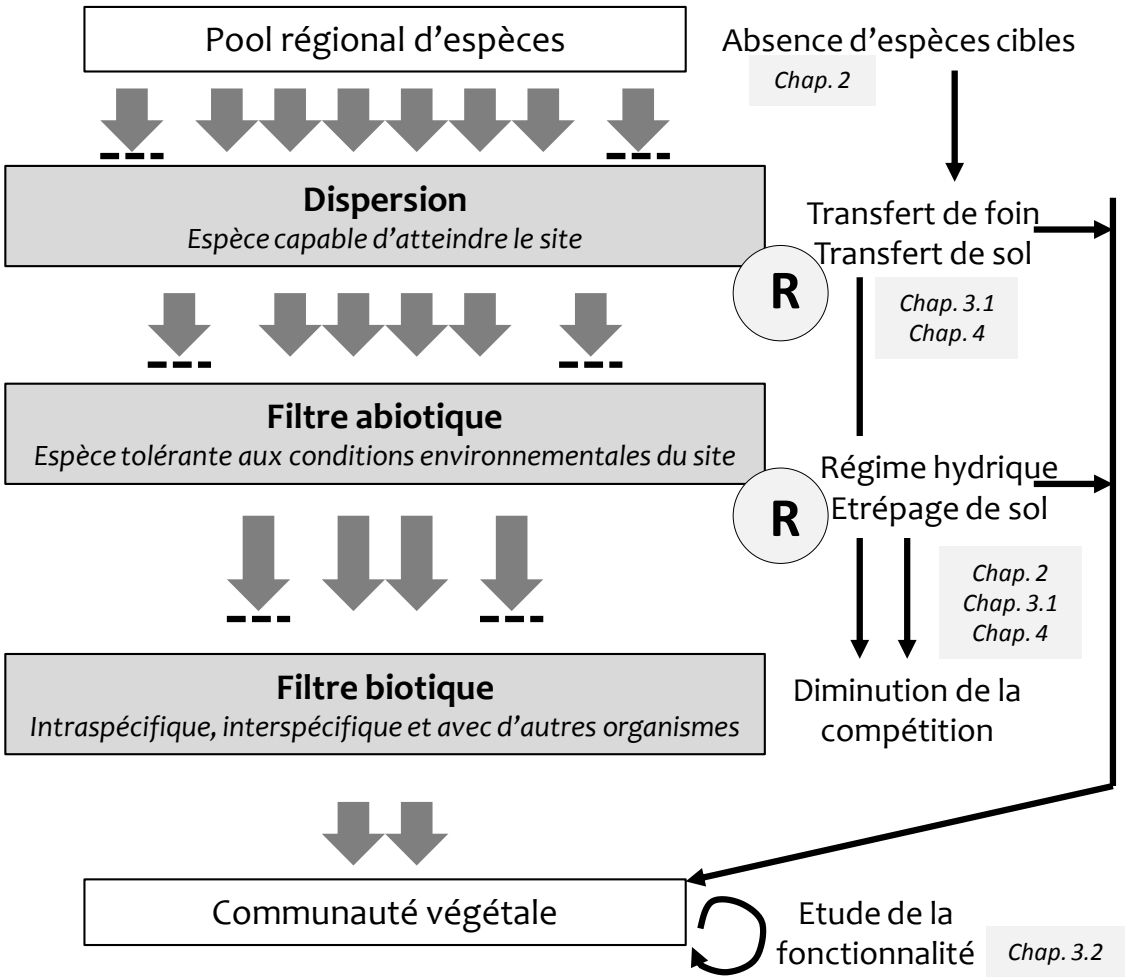

Figure D.2 : Principaux résultats des actions de restauration acquis dans le ***chapitre 2***, ***chapitre 3.1***, ***chapitre 3.2*** et ***chapitre 4*** replacés dans le modèle de filtre de l'assemblage des communautés.

D.1.2. Effets de priorité dans les communautés végétales

Malgré la dominance de la théorie déterministe dans le modèle d'assemblage des communautés, de récentes études s'accordent à mettre en évidence le rôle crucial des contingences historiques sur l'assemblage des communautés (Chase 2003; Fukami et al. 2005; Ejrnæs et al. 2006; Lulow 2006; Trowbridge 2007; Körner et al. 2008; Collinge and Ray 2009; Fukami and Nakajima 2011; Wainwright et al. 2012; Kardol et al. 2013). Ces événements stochastiques peuvent être à l'origine de divergence dans la trajectoire des communautés, même sous des conditions environnementales similaires. La présence initiale d'une espèce peut en effet grandement influencer l'établissement des espèces suivantes (i.e. effets de priorité ; Young et al. 2005; Fukami et al. 2005).

Ces espèces « clés » ou « ingénieurs » (Jones et al. 1994; Brown 1995; Stone 1995) ont un rôle dans l'assemblage des communautés, souvent lié à leur importante biomasse. Installer ces espèces capables de favoriser la présence d'autres espèces cibles, semble une démarche prometteuse en restauration. La présence de ces espèces en début de succession pourrait également être un bon indicateur du devenir de la communauté, leur présence influant fortement sur l'issue de la restauration de la communauté végétale (cf ***Discussion section D.3.3***).

L'utilisation des interactions biotiques positives (i.e. la facilitation) en restauration écologique a déjà été testée à travers le semis d'espèces nurses (Aerts et al. 1995; Verhagen et al. 2001; Coiffait-Gombault et al. 2012; Jaunatre et al. 2012), limitant les espèces indésirables, utilisant l'excès d'azote et de phosphore dans le sol et qui favorisent ainsi l'installation des espèces cibles.

Les études préliminaires sur les effets de priorité (***Transition to Discussion section TD.3***) ont été mises en place à partir d'observations réalisées sur le terrain, et indiquent que ces effets de priorité pourraient exister sur notre terrain, où certaines espèces cibles, par leur structuration et leur biomasse, semblent agréger autour d'elle les autres espèces présentes dans le transfert de foin (***Figure D.3***).

Les résultats concernant la richesse spécifique (***Transition to Discussion section TD.2***) montrent une simple corrélation entre cette richesse et la présence de quelques espèces cibles (i.e. *Scorpiurus muricatus* L., *Hedypnois cretica* Willd et *Brachypodium distachyon* (L.) P.Beauv.) ne permettent pas de conclure sur un effet facilitateur. Un simple effet site (i.e. bonnes conditions environnementales permettant une augmentation de la richesse spécifique) pourrait également être à l'origine de cette corrélation positive. Diverses études ont cependant montré qu'une agrégation de deux espèces était souvent due à de la facilitation et non à des conditions abiotiques de microsites (Tirado and Pugnaire 2005; Maestre et al. 2008). Les relevés de végétation, réalisés dans la restauration à plus large échelle et utilisés pour ces calculs de corrélations et dans la mise en évidence de ces corrélations, ne permettent pas d'affirmer si des phénomènes de facilitation sont à l'origine de ces corrélations positives. En effet, la taille des quadrats d'échantillonnage (50 x 50 cm) est trop grande pour mettre en évidence de la facilitation : les espèces peuvent être présentes dans le même quadrat tout en étant éloignées l'une de l'autre, la

cooccurrence ne pouvant pas alors être attribuée à des interactions biotiques positives, uniquement mesurable à une échelle spatiale plus petite (cf ***Discussion section D.4.2***; Gotelli and McCabe 2002; Tirado and Pugnaire 2005; Maestre et al. 2008).

Figure D.3: Photographie d'une agrégation de *Trifolium resupinatum* L., *Brachypodium distachyon* (L.)P.Beauv, *Filago pygmaea* L., *Parapholis filiformis* ***(Roth) C.E.Hubb. autour de*** *Scorpiurus muricatus* ***L.***

D.1.3. Les objectifs de restauration sont-ils atteints ?

Il est évidemment trop tôt pour conclure sur la possibilité pour les communautés en cours de restauration d'atteindre les communautés de référence. A la lumière de nos expérimentations et du suivi de courte durée, restaurer un marais temporaire ou une pelouse meso-xérique sur des friches rizicoles semble nécessiter la manipulation des trois filtres : dispersion, conditions environnementales et interactions biotiques, afin de positionner rapidement les communautés sur la trajectoire des communautés de référence. La restauration des communautés aquatiques *via* la manipulation de ces trois filtres (***chapitre 3.1***) montre des résultats plus convaincants en terme de similarité avec les communautés de référence, de nombre d'espèces cibles et d'espèces non désirées par

rapport à la restauration de la communauté terrestre (***chapitre 4***), où la compétition conduit dès la deuxième année à la diminution de la richesse spécifique et de la richesse en espèces cibles.

D.2. Différentes réponses dans la dynamique végétale

D.2.1. Différence entre les communautés aquatiques et les communautés terrestres

Nos expérimentations en mésocosmes suggèrent qu'il est plus facile de réintroduire les espèces cibles des marais que celles des pelouses. Cette différence pourrait, pour une large part, s'expliquer par les conditions abiotiques probablement plus proches des conditions de référence pour les marais que pour les pelouses. De façon générale, il paraît plus aisé de restaurer le principal filtre abiotique des marais temporaires (i.e. le régime hydrique ; Grillas 1990; Zedler 2000a) que celui des pelouses méso-xériques (i.e. sol oligotrophe; Lepš 1999; Kiehl et al. 2010) en particulier dans un contexte post-cultural. La capacité prédictive augmente avec le niveau de contrainte du milieu (Mesléard et al. 1991) et les communautés aquatiques sont plus prédictibles, de par leur conditions abiotiques drastiques qui les sélectionnent d'avantage. A l'inverse, dans les communautés terrestres, la prédictibilité est d'autant plus perfectible que les conditions sont peu limitantes et n'opèrent pas d'effets sélectifs forts.

Les communautés végétales des pelouses sont d'autre part soumises à un niveau de compétition élevée résultant de la présence de nombreuses espèces non désirées favorisées par le niveau trophique du sol. Ce n'est pas le cas pour les communautés aquatiques où aucune espèce susceptible de rentrer en compétition avec la communauté cible n'a été détectée dans le pool régional. Sachant que la zoochorie à l'origine d'une forte dispersion de graines d'espèces de marais temporaires est hautement prévisible à long terme (Figuerola and Green 2002a; Brochet et al. 2010a), la question de devoir transférer des propagules doit être posée, sachant qu'aucune phase de blocage à contrecarrer ne semble exister. Le transfert de propagules représente un coût humain et financier supplémentaire. Dans le cas des marais temporaires, il ne semble qu'accélérer le développement de la communauté cible et faciliter la présence de certaines espèces rares (plus difficile à obtenir avec la colonisation spontanée). Pour autant, la mise en place de la

restauration à large l'échelle nous invite cependant à être prudents quant à toute conclusion hâtive. En effet, à cette échelle, et contrairement à nos observations dans les mésocosmes, les algues filamenteuses *Cladophora vagabunda (L.) Hoek* (absentes du pool régional d'espèces, car la méthodologie utilisée ne permet pas de détecter leur spores de taille inférieur à 100 µm ; ***chapitre 2***), peuvent gêner le plein développement nos espèces cibles.

D.2.2. Différence entre restauration en mésocosme et à plus large échelle

L'étrépage de sol, la restauration du régime hydrique et le transfert de sol à plus large échelle (4000m² ; ***Transition to Discussion section TD.1***) n'aboutissent pas à des résultats aussi convaincants qu'en mésocosmes (***chapitre 3.1***). La totalité des espèces transférées n'apparaît pas dans le marais restauré et une diminution de l'abondance relative des espèces cibles dans la communauté (55% d'espèces cibles à large échelle *vs*. 75% en mésocosme) indique que la restauration apparaît plus complexe. L'omniprésence d'algues filamenteuses (*Cladophora vagabunda (L.) Hoek*) sur toute la surface du marais restauré, semble défavorable à l'installation de la communauté présente dans le transfert de sol. La présence de cette algue, déjà mise en évidence dans les mésocosmes (***chapitre 3.1***) mais dont aucun effet n'avait été détecté, semble compromettre l'établissement des espèces transférées à large échelle. Naturellement présentes dans les marais de référence en octobre à la première mise en eau et en mai durant les premières chaleurs, ces algues n'y influencent pas l'expression des macrophytes cibles et diminuent avec l'augmentation de l'abondance de ceux-ci. Dans les marais restaurés, leur présence pourrait être liée à un relargage de nutriments favorisé par la mise en suspension du sédiment. D'autres études sur le transfert de sol (Bullock 1998; Jaunatre et al. 2012) indiquent une modification de la communauté causée par la perturbation induite par le transfert de sol. Le transfert de sol mis en place tardivement ainsi qu'une mise en eau également tardive ont aussi pu contribuer à l'installation durable de ces algues.

A l'inverse, la restauration des communautés de pelouses méso-xériques à plus large échelle (3000 m² ; ***Transition to Discussion section TD.2***) montre par rapport à la restauration des mésocosmes (***chapitre 4***), relativement petits, une augmentation de l'abondance relative des espèces cibles dans la communauté (60% d'espèces cibles à large

échelle *vs.* 46% en mésocosme). Cette amélioration de résultats peut s'expliquer par la diminution à cette échelle des effets de bords, qui entrainent la rapide colonisation des espèces non désirées (Rasran et al. 2007).

Même si les résultats d'écologie de la restauration à faible échelle (d'espace et de temps) permettent de dessiner les lignes directrices et de tester les outils à mettre en place pour la restauration à plus large échelle (Hagen and Evju 2013), ils ne permettent pas de prédire l'exact déroulement des mécanismes (Zedler 2000a). L'incertitude et la complexité des milieux vivants rendent difficiles la prédiction et encore d'avantage lorsque la taille de l'objet d'étude s'agrandit. A l'échelle de l'écosystème rentre en jeu un grand nombre de variables non maitrisées et souvent non prises en compte. La restauration à cette échelle nécessite ainsi une gestion adaptative, qui repose sur une logique d'apprentissage, d'amélioration pas-à-pas où les actions sont régulièrement ajustées (Holling 1978; Olsson et al. 2004).

D.3. De l'écologie de la restauration à la restauration écologique : propositions et recommandations

D.3.1. Matériel végétal transféré

Dans nos expériences de transfert de foin (***chapitre 4***) et de sol (***chapitre 3.1***), l'accent a été mis sur la qualité du matériel végétal transféré, cette qualité pouvant avoir d'importantes conséquences sur les résultats de la restauration. Plus le matériel végétal transféré correspond à la communauté de référence en termes de richesse spécifique et d'abondance, plus les résultats de la restauration sont prédictibles (Török et al. 2011b). Concernant le matériel des communautés de pelouses, différentes techniques de prélèvement ont été utilisées et à diverses périodes, maximisant ainsi le nombre d'espèces cibles prélevées (démontré dans les etudes de Stevenson et al. 1995; Stevenson et al. 1997; Kiehl et al. 2006). Le sol utilisé pour les communautés aquatiques a lui été collecté sur différents marais temporaires, permettant de représenter la gamme de variations environnementales (i.e. période d'inondation et salinité) et donc de communautés végétales, correspondant à la gamme des conditions susceptibles d'être rencontrées sur le site du Cassaïre. Le fait de prélever dans plusieurs marais temporaires

vise à créer un effet de stockage de la banque de graines des marais temporaires (storage effect ; Bonis et al. 1995; Cáceres 1997; Bonis 1998), mécanismes permettant de répondre à des changements de conditions environnementales et à des populations de coexister dans le temps.

Plusieurs études (Holling and Meffe 1996; Simenstad and Thom 1996; Moreno-Mateos et al. 2012; Español et al. 2012) ont mis en évidence une plus forte vulnérabilité aux perturbations des zones humides restaurées et une gamme de variations plus réduite par rapport aux zones humides naturelles. Maximiser la diversité spécifique des milieux restaurés peut donc potentiellement offrir une capacité de réponses à des changements environnementaux, une complexité et une résilience plus grande (Tilman et al. 2006).

La restauration pourrait être améliorée en épandant directement, après récolte, le matériel, ce qui éviterait des pertes en graines inhérentes au séchage et au stockage (Török et al. 2011b) et augmenterait le taux d'établissement des espèces transférées (Kiehl et al. 2010). La quantité de matériel mais aussi la fréquence d'ensemencement est un facteur influençant le résultat de restauration. Le début de suivi du transfert de foin sur une plus large échelle (***Transition to Discussion section TD.2***) ne suggère pas d'effet de la densité sur la richesse spécifique globale ni sur le nombre d'espèces cibles. Augmenter la fréquence d'ensemencement devrait permettre d'augmenter le recrutement et le maintien des espèces transférées (Collinge and Ray 2009).

Si la quantité et la qualité du matériel végétal transféré sont des facteurs importants dans la réussite de la restauration, la lourdeur des activités et le coût potentiel de la restauration peuvent également limiter la réalisation de projets. La réduction des coûts et de l'énergie dépensée semble possible en jouant sur les superficies d'ensemencement ou en sélectionnant d'avantage les espèces à introduire par le seul transfert de quelques espèces clés qui, par effet de priorité, faciliteraient l'obtention de la communauté de référence. Tester ces différents facteurs permettrait probablement de proposer des techniques de restauration présentant un bon compromis coût-résultat.

D.3.2. Superficie d'ensemencement

Par le développement d'un couvert végétal dense, l'ensemencement de la totalité de la superficie à restaurer semble à priori mieux à même de limiter le recrutement par des

espèces non désirées. Cependant, un tel apport, compte-tenu des coûts impliqués (notamment en main d'œuvre), semble difficilement réalisable sur de grande superficie. D'autre part la collecte qui en résulte est susceptible d'endommager les écosystèmes donneurs (i.e. les écosystèmes de référence). Sous l'hypothèse que la zone inoculée/semée fonctionne comme source d'espèces cibles pour la colonisation spontanée des régions voisines non ensemencées (Hölzel and Otte 2003; Jongepierová et al. 2007; Rasran et al. 2007; Kiehl et al. 2010; Török et al. 2011b; Aradottir 2012; Mitchley et al. 2012), réduire les superficies sur lesquelles sont introduites ces propagules diminuerait les coûts sans pour autant impacter significativement les résultats, à terme, de la restauration.

Un parallèle peut être fait avec les réflexions concernant la délimitation des réserves naturelles et le débat sur le SLOSS (Single Large Or Several Small ; Soulé and Simberloff 1986), dans lequel il s'agit de savoir s'il est préférable de protéger un unique grand espace ou plusieurs petits. Même si le débat n'est pas résolu, la réponse semble essentiellement dépendre de l'espèce considérée. Dans le cas des communautés végétales, la question peut se résumer de façon pratique à savoir s'il est préférable d'introduire des propagules sur une partie de la surface à restaurer et dans ce cas de quelle façon les introduire (i.e. design d'introduction avec le même type de réflexion que sur le SLOSS) ou au contraire s'il est préférable d'introduire des propagules sur la totalité de la superficie. Le fait de ne devoir introduire des propagules que sur une partie du site repose sur la capacité des espèces cibles à coloniser les espaces non ensemencés/inoculés (i.e. fonction source ou effet de nucléation des zones ensemencées/inoculées ; Reis et al. 2003). Les parties non ensemencées/inoculées pourraient cependant constituer des fenêtres d'invasion pour les d'espèces indésirables (Johnstone 1986), rendant la communauté transférée plus perméable aux espèces non désirées, la compétition aboutissant à un effet contraire à celui escompté. Dans notre cas, les premiers résultats des tests sur le design d'introduction (i.e. ensemencer la même quantité de matériel sur une bande ou sur deux bandes, cf ***Transition to Discussion***) ne montrent aucune différence en termes de richesse spécifique globale et en espèce cibles, ni pour les communautés aquatiques, ni pour les communautés terrestres (***Transition to Discussion***). De même, aucune différence n'est observée lorsque l'on considère la proportion de la superficie ensemencée (i.e. 100% de la

superficie *vs.* 50 %de la superficie pour les pelouses et 100% de la superficie *vs.* 1/3 de la superficie pour les marais; ***Transition to Discussion***). Si un suivi sur le long terme est nécessaire pour tirer des conclusions, ensemencer la totalité de la superficie à restaurer ne semble pas nécessaire, au vu de nos premiers résultats.

D.3.3. Effets de priorité

Le succès de restauration est souvent évalué sur un court laps de temps, par absence de suivi sur le long terme (Fahselt 2007), cette évaluation rendant les prédictions quant au devenir des communautés en cours de restauration moins fiables. Cette difficulté pourrait être partiellement contournée en utilisant les espèces connues pour leur effet de priorité. L'identification d'espèces facilitatrices et la bonne connaissance de leur rôle structurant devraient permettre (i) d'obtenir un indicateur relativement grossier mais précoce du potentiel succès de restauration (i.e. si l'espèce est présente il y a plus de chance d'obtenir notre communauté de référence que si elle est absente) et (ii) de réduire le coût des traitements de restauration (limitation des prélèvements alors focalisés sur ces espèces) et potentiellement celui du suivi (l'unique détection de ces espèces, de leur nombre et de leur répartition, sans pour autant devoir caractériser toute la communauté).

Les effets de priorité paraissent notamment concerner certaines espèces des pelouses méso-xériques (i.e. *Scorpiurus muricatus* L., *Hedypnois cretica* Willd et *Brachypodium distachyon* (L.) P.Beauv.) identifiées comme possible facilitatrices des espèces cibles (cf ***Transition to Discussion***). Dans le cas des marais temporaires, introduire des espèces telles que *Ranunculus peltatus* Schrank pourrait diminuer la présence des algues filamenteuses qui semble être problématique dans l'établissement de nos espèces cibles inoculées à l'échelle du marais (***Figure D.4***). En effet, cette espèce à phénologie variable, peut germer très précocement, s'installe aisément, tolère des assecs estivaux marqués et recouvre la surface de l'eau (Garbey et al. 2004; Mouronval and Baudouin 2010), empêchant ainsi la présence des algues filamenteuses. Cette espèce qui rend le plan d'eau stable et moins turbide, disparaît d'autre part rapidement au cours de la saison, ne posant probablement pas de problèmes à de nombreux macrophytes commençant leur développement plus tardivement en saison.

***Figure D.4**: Photographie du marais restauré à large échelle avec la présence d'algue filamenteuse Cladophora vagabunda (L.) Hoek sur toute la surface du plan d'eau et d'une renoncule peltée Ranunculus peltatus* Schrank*, qui pourrait être utilisée pour diminuer la présence de Cladophora vagabunda (L.) Hoek.*

La seule introduction de ces espèces clés pourrait ne pas suffire pour atteindre les objectifs de restauration (i.e. aboutir à des communautés proches de celles de référence). Leur présence semble néanmoins faciliter l'établissement d'autres espèces. Un choix judicieux comprenant des espèces clés combinées à un matériel végétal contenant d'autres espèces de la communauté pourrait permettre d'obtenir les communautés souhaitées sans pour autant nécessiter des quantités de matériel importantes importantes.

Afin de satisfaire au compromis « coût-résultat », qui guide la majorité des projets de restauration, varier la superficie d'ensemencement en fonction des attributs des espèces, comme le préconisent Pakeman et al. (2002) paraît donc une démarche souhaitable. Les espèces identifiées comme espèces clés, à l'origine des effets de priorité, seraient réintroduites sur la totalité de la zone à restaurer et le reste du matériel végétal

contenant les autres espèces cibles (foin ou sol) pourrait être transféré par taches, la capacité de colonisation de ces espèces non clés du matériel végétal étant assurée par les conditions générées par les espèces clés (e.g. diminution des espèces non désirées par couvert végétal et donc diminution de la compétition, piégeage de propagules, restauration de conditions abiotiques adaptées). Dans ce cas, le transfert du matériel végétal des espèces non clés semble devoir être réalisé dans un laps de temps assez court après l'introduction des premières espèces clés.

Ces différentes recommandations pour la pratique de restauration à large échelle, qui doivent être encore testées dans notre cas, si elles conduisent à diminuer le coût de la restauration, permettraient également d'obtenir une meilleure acceptation du public (Miller and Hobbs 2007).

D.3.4. Intégration de l'ensemble de l'écosystème dans l'évaluation de la restauration

Dans nos expérimentations nous avons mis en évidence des différences de réponses à la restauration entre les invertébrés aquatiques et les macrophytes (***chapitre 3.2***), la colonisation spontanée par les invertébrés étant plus rapide que celle des macrophytes (cf ***Transition to Chapter 4***). De telles différences dans les réponses entre compartiments de l'écosystème, déjà mis en évidence par des études précédentes (Trexler 1995), doivent être prises en compte dans les choix d'indicateurs d'évaluation. Cette intégration de plusieurs compartiments de l'écosystème apporte des indications complémentaires sur la fonctionnalité de ces communautés végétales restaurées (***Figure D.1*** et ***Figure D.2***).

Cette thèse en écologie des communautés, écologie de la restauration et restauration écologique (***Tableau D.1.***) ne constitue qu'une étape et appelle à de nouvelles recherches dont les questions sont exposées dans le paragraphe suivant (***Tableau D.1.***).

Tableau D.1: Principaux résultats en écologie des communautés, en écologie de la restauration et en restauration écologique. Les perspectives de recherche sont indiquées en italique.

Contribution à l'écologie des communautés
- La composition de la végétation est d'avantage corrélée à la composition de la banque de graines qu'à la composition de la pluie de graines. Quand la densité de la banque de graines diminue, la pluie de graines peut plus facilement s'exprimer dans la végétation (Chapitre 2)
- Les rôles des filtres abiotique et de la dispersion sont déterminants en début de succession dans l'assemblage des communautés (Chapitre 3.1 et chapitre 4)
- Le filtre biotique joue un rôle important dans le devenir de la communauté végétale, surtout quand les conditions abiotiques sont moins contraignantes (Chapitre 3.1 et chapitre 4)
- La colonisation spontanée des communautés d'invertébrés aquatiques est plus efficace que celle des communautés végétales (Chapitre 3.2)
- Les effets de priorités peuvent influencer l'assemblage des communautés en début de succession (Transition à la discussion)
Contribution à l'écologie de la restauration
- La prédictibilité de succès de restauration peut se mesurer à travers la contrainte exercée par le filtre abiotique (Chapitre 3.1 et chapitre 4)
- La manipulation du filtre abiotique est indispensable mais insuffisante pour les deux communautés (chapitre 2)
- La manipulation du filtre abiotique et de la dispersion est suffisante pour restaurer les communautés aquatiques (Chapitre 3.1)
- La manipulation du filtre abiotique et de la dispersion est insuffisante pour restaurer les communautés terrestres et doit être combinée à une diminution de la compétition (Chapitre 4)
- L'évaluation de la restauration ne doit pas se baser surune seule composante de l'écosystème (Chapitre 3.2)
- L'effet du pâturage sur les communautés terrestres doit être testé
- Les espèces clés liées à des effets de priorités doivent être identifiées avec des modèles nuls
Contribution à la restauration écologique
- L'étrépage de sol, le transfert de foin et le transfert de sol apparaissent comme des techniques de restauration pertinentes (Chapitre 3.1 et chapitre 4)
- L'introduction du matériel végétal sur toute la superficie de la zone à restaurer n'est pas nécessaire (Transition à la discussion)
- Les différences de résultats à petite échelle expérimentale et à l'échelle d'un écosystème dans la restauration doivent être pris en compte via une gestion adaptative (Transition à la discussion)
- D'autres composantes de l'écosystème doivent être intégrées dans l'évaluation du succès de restauration (Chapitre 3.2)
- L'activité de chasse peut être pris en compte pour évaluer la part sociale
- Le transfert de sol combiné à l'inoculation de Ranunculus peltatus pour limiter les algues filamenteuses doit être testé
- Le semis d'espèces clés sur toute la superficie combiné à l'inoculation de foin par taches doit être testé

D.4. Perspectives de recherche sur le site du Cassaïre

D.4.1. Filtre biotique

Nous avons souligné l'importance du filtre biotique dans l'assemblage des communautés. Cependant ce rôle n'a pas été directement testé dans nos expérimentations. L'importance du pâturage a déjà été mis en évidence dans différents travaux sur les pelouses et les friches rizicoles, son action permettant de diminuer la compétition avec les espèces non désirées et d'augmenter significativement la richesse spécifique (Mesléard et al. 1991; Mesléard et al. 1999; Coiffait-Gombault et al. 2011). Tester l'effet du pâturage en particulier ovin et équin selon différentes modalités (charge, période, durée, fréquence) sur les pelouses méso-xérique restaurées permettrait (i) de mettre indirectement en évidence l'effet de la compétition par les espèces non désirées dans la restauration des communautés végétales ii) de déterminer la ou les gestions *ad hoc* contribuant au bon maintien des communautés sur les bonnes trajectoires.

D.4.2. Effets de priorité

Afin d'affirmer que les corrélations mises en évidence entre certaines espèces et la richesse spécifique (***Transition to Discussion section TD.3***) peuvent être associées à des phénomènes de facilitation, une lecture plus fine de la végétation doit être mise en place. Dans ce sens, le suivi de végétation tel qu'utilisé par Maestre et al. (2008) (i.e. quadrats réalisés à l'échelle des interactions potentielles de 5 cm × 5 cm), où la présence de chaque individu est notée, pourrait aider à la mise en évidence de telles interactions. L'utilisation de modèles nuls pour générer des communautés aléatoires non structurées par les interactions biotiques permettrait en les comparant à nos communautés et en utilisant différents indices de cooccurrence (voir Gotelli 2000 pour les détails des indices pouvant être utilisés) de tester indirectement des effets de facilitation (coexistence des espèces au sein d'un même quadrat plus forte qu'attendue aléatoirement). Il pourrait être bénéfique de compléter les mesures de cooccurrence par des expériences d'introduction d'espèces à priori facilitatrices, qui permettraient ainsi de s'affranchir d'un effet de simple corrélation entre micro-habitat favorable, présence de ces espèces et augmentation de la

richesse spécifique. Ainsi de façon concrète dans notre cas, compléter le transfert de sol par l'ensemencement de graines de *Ranunculus peltatus* Schrank permettrait de tester le rôle de cette espèce dans la diminution des algues filamenteuses des marais (cf hypothèse ***Discussion section D.3.3.***).

La connaissance des traits fonctionnels des espèces identifiées comme facilitatrices complèterait la compréhension des processus de facilitation. Ces espèces pourraient par exemple i) accumuler plus facilement les graines d'autres espèces, ii) modifier le micro-habitat ou iii) éliminer les espèces non cibles. *Scorpiurus muricatus* L. identifiée dans les résultats préliminaires (***Transition to Discussion section TD.3***), pourrait modifier l'habitat *via* la fixation de l'azote (Famille des Fabacées).

D.4.3. Approche services écosystémique dans l'évaluation

L'évaluation par une approche communauté (richesse spécifique mais aussi structure et composition de la communauté avec le développement de nouveau indicateur de restauration cf ***Annexe 1***; Jaunatre et al. 2013b) permet, pour partie, d'évaluer la stabilité d'un écosystème face à des modifications environnementales (Reinartz and Warne 1993; Tilman et al. 2006), elle ne reflète cependant qu'un compartiment de l'écosystème. L'avifaune peut apparaître également comme un indicateur de restauration à priori plus aisé à mesurer que les communautés d'invertébrés. La pertinence de cet indicateur a cependant été contesté et l'utilisation de ce seul indicateur ne permet pas de juger de la qualité d'un habitat (Christian et al. 2009): un marais de chasse géré de façon opposée aux conditions naturelles peut être fortement fréquenté par certains types d'oiseaux d'eau mais se révéler pauvre d'un point de vue de la végétation (Tamisier and Grillas 1994; Aznar et al. 2003). Dans notre cas, la composante avifaune sera de toute façon un critère d'évaluation notamment pour l'activité cynégétique, i.e. un marais de chasse offrant une diversité et une abondance d'oiseaux d'eau chassables. L'évaluation du niveau de restauration à travers les services écosystémiques apparaît judicieuse (Bakker et al. 2000; Findlay et al. 2002; Palmer and Filoso 2009) notamment dans des socio-écosystèmes restaurés où une démarche participative est à l'origine du projet de restauration. Ainsi, évaluer la fonction chasse (fréquentation par les chasseurs/tableau de chasse) sur le

Cassaïre est aussi un des critères jugeant de l'efficacité du projet de restauration et de sa part sociale.

La restauration à l'échelle du marais et la mise en place de la première année de chasse en septembre 2012, sont trop récentes pour qu'une évaluation dans ce sens puisse être faite. Cependant, à plus long terme, l'évaluation de la fonction de chasse, avec la mise en perspective des tableaux de chasse et de la richesse spécifique en macrophytes du marais restauré, comparée aux marais de chasse traditionnels, devrait permettre en fonction des résultats, de promouvoir des remises en eau des marais plus tardives. Ces mises en eau plus tardives si, comme nous le pensons, peuvent assurer une activité cynégétique jugée convenable par les chasseurs et si ces mises en eau plus tardives devenaient socialement acceptables voire bénéfiques (tableau de chasse, économie dans la gestion de l'eau) pourraient contribuer à réduire la prolifération d'espèces invasives, fréquentes dans les marais de chasse à mise en eau estivale.

L'approche service écosystémique ne peut cependant se substituer à des approches plus traditionnelles visant la protection de la biodiversité (e.g. espèces patrimoniales, espèces en danger, communauté de référence) et doit être utilisée de façon complémentaire à d'autres indicateurs comme ceux utilisés par exemple dans cette thèse. Les risques d'une démarche centrée sur les services écosystémiques, mettant en exergue une vision non holistique mais utilitariste de l'écosystème, ont d'ailleurs été largement exposés (Maris, 2010).

D.5. La place de la restauration écologique dans la société

Les expérimentations réalisées dans le cadre de cette thèse ont permis de tester des techniques de restauration *a priori* pertinentes à large échelle. Elles soulignent néanmoins la difficulté dans la restauration à appréhender plusieurs compartiments de l'écosystème et *a fortiori* sa globalité. La perfectibilité des suivis de restauration entraîne souvent une surestimation des gains de restauration (***Chapitre 3.2***, Regnery 2013). Un suivi à long terme et la mise en place de différents indicateurs sont indispensables. Notre évaluation sur trois années ne concerne que le début de la restauration, elle est donc partielle et discutable. Elle coïncide néanmoins avec celle d'autres études, indiquant qu'un retour à

l'état de référence est quasi-impossible (Holling and Meffe 1996; Fahselt 2007; Benayas et al. 2009; Jaunatre 2012) mais souligne le bénéfice de la restauration pour la biodiversité. L'écologie de la restauration apparaît donc bien comme un moyen pour maintenir la biodiversité et contrôler son érosion.

Cependant, cette discipline est actuellement au centre de débats (Elliot 1982; Maris et al. 2010) et provoque des craintes, en particulier sur son recours dans les projets d'aménagements. Cette discipline dévaluerait et instrumentaliserait la nature et, loin de contribuer aux objectifs définis par le plan stratégique pour la biodiversité (Convention on Biological Diversity 2011), favoriserait, par effet pervers, la destruction des espaces naturels. De nombreux projets de restauration écologique voient le jour dans le cadre de mesures compensatoires suite au développement de projets d'aménagements (Dunkerque LNG 2013; Dutoit and Oberlinkels 2013). La compensation écologique est la dernière étape de la séquence « Eviter, Réduire, Compenser » (i.e. ERC) prévu par la législation française dans le cas d'impact sur des espaces naturels. Comme l'indique son nom, le but est de compenser les pertes, à travers des opérations d'acquisition ou de restauration (Regnery 2013), pour atteindre des objectifs écologiques de zéro perte nette. A ce titre, la multiplication de projets de restauration exclusivement financés dans le cadre de mesures compensatoires en particulier avec la mise en place récente de banques d'actifs naturels (i.e. mécanisme de compensation par l'offre) (e.g. Réserves d'Actifs Naturels mis en place par la CDC Biodiversité sur le projet Cossure (Chabran and Napoléone 2013), opération expérimentale d'offre de compensation sur le site de Combe Madame, initié par EDF (EDF 2013)) risquerait d'amoindrir les deux premiers volets du triptyque ERC, et peuvent constituer une dérive vers la marchandisation de la biodiversité. Les services instructeurs de l'Etat contrôlent le travail d'évitement ou de réduction avant la mise en œuvre de compensation, mais de nombreux exemples témoignent de l'existence de failles dans l'application de cette séquence (Chabran and Napoléone 2013). Les questions posées par ces dérives potentielles correspondent très exactement à certaines questions posées dans notre travail « quel est le gain de biodiversité en restauration ? », « comment l'évaluation de cette restauration est-elle prise en compte ? », « peut-on considérer qu'il n'y a pas de perte nette ? » et nécessitent bien évidemment des réponses.

L'écologie de la restauration ne doit pas se substituer à la protection de milieux naturels, et justifier leurs destructions, mais venir en complément aux efforts de conservation qu'il convient de consolider (Fahselt 2007).

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Annexes

Annexe 1: New synthetic indicators to assess community resilience and restoration success. Ecological indicators. Jaunatre et al., 2013b.

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New synthetic indicators to assess community resilience and restoration success

Renaud Jaunatre [a,*], Elise Buisson [a], Isabelle Muller [a,b], Hélène Morlon [c], François Mesléard [a,b], Thierry Dutoit [a]

[a] Université d'Avignon et des Pays de Vaucluse, UMR CNRS/IRD 7263/237 Institut Méditerranéen de Biodiversité et d'Ecologie, France
[b] Centre de recherche de la Tour du Valat, France
[c] Centre de Mathématiques Appliquées, École Polytechnique, Palaiseau, France

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ABSTRACT

The Strategic Plan for Biodiversity 2011–2020 sets as an objective the restoration of 15% of degraded ecosystems by 2020. This challenge raises at least two major questions: (i) How to restore and (ii) how to measure restoration success of said ecosystems? Measurement of restoration success is necessary to assess objective achievement and to adjust management with regard to objectives. Numerous studies are being conducted to try to work out synthetic indices to assess ecosystem diversity or integrity in the context of global change. Nevertheless, at the community level, there is no index that allows the assessment of community integrity regarding its restoration or resilience, despite the fact that a lot of indicators are used such as species richness, Shannon diversity, multivariate analyses or similarity indices. We have therefore developed two new indices giving new insights on community states: the first index, coined as the Community Structure Integrity Index, measures the proportion of the species abundance in the reference community represented in the restored or degraded community, and the second index, coined as the Higher Abundance Index, measures the proportion of the species abundance in the restored or degraded community which is higher than in the reference community. We illustrate and discuss the use of these new indices with three examples: (i) fictitious communities, (ii) a recent restoration (2 years) of a Mediterranean temporary wetland (Camargue in France) in order to assess restoration efficiency, and (iii) a recently disturbed pseudo-steppe plant community (La Crau area in France) in order to assess natural resilience of the plant community. The indices provide summarized information on the success of restoration or on the resilience of the plant community, which both appear less positive than with standard indicators already used. The indices also provide additional insights useful for management purposes: the Community Structure Integrity Index can indicate whether the improving target species abundance is needed or not while the Higher Abundance Index can indicate whether controlling the high abundance of some species is needed in order to approach a reference ecosystem. These relatively simple indices developed on community composition and structure state can provide a base to further indices focusing on ecosystem functioning or services not only calculating values as a static point but also its temporal or spatial dynamic.

1. Introduction

The Strategic Plan for Biodiversity 2011–2020 sets as an objective the restoration of 15% of degraded ecosystems by 2020 (Convention on Biological Diversity, 2011), and this challenge raises at least two major questions: (i) How to restore and (ii) how to measure restoration success of said ecosystems? The first question has been addressed and is still being addressed in a multitude of ecological systems and geographical areas (see for example (Perrow and Davy, 2002)) and for various restoration aims. Restoration targets are diverse: from rehabilitation, which is the restoration of one or some target ecosystem functions, to the restoration *sensu stricto*, which is the restoration of the whole ecosystem, i.e. its richness, composition, structure and functions (Society for Ecological Restoration International Science and Working Policy Group, 2004). Restoration is advocated for stopping the global erosion of biodiversity (Millennium Ecosystem Assessment, 2005; Nellemann et al., 2010), and is imposed by law in many countries for ecosystem destruction or degradation offsets (ten Kate et al., 2004). However, a recent meta-analysis conducted over 89 ecological restoration projects

Abbreviations: CSII, Community Structure Integrity Index; $CSII_{norm}$, normalized Community Structure Integrity Index; HAI, Higher Abundance Index.

* Corresponding author at: IUT, Site Agroparc, BP 61207, 84911 Avignon Cedex 9, France. Tel.: +33 4 90 84 38 58; fax: +33 4 90 84 38 67.
E-mail address: renaud.jaunatre@yahoo.fr (R. Jaunatre).

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concluded that although restored ecosystems provide more biodiversity and ecosystem services than degraded ecosystems, these parameters still do not reach those of reference ecosystems (Benayas et al., 2009).

A community is defined as "an assemblage of populations of living organisms in a prescribed area or habitat" (Krebs, 1972). A multitude of indicators can be used to characterize a community (e.g. patchiness, nutrient cycling rate, interaction intensities, etc. (Noss, 1990)). To assess restoration success, most measures of biodiversity are related to abundance, species richness, diversity, growth, or biomass of organisms (Ruiz-Jaen and Aide, 2005). As strengthened by the analysis of 80 recent (2007–2011) papers comparing restored and reference communities, species richness and abundances are the most commonly used indicators of restoration (Appendix B). Species-richness is one of the simplest ways to describe a community (Magurran, 2004), however, many authors admit that species-richness, as well as diversity index (Shannon, Pielou, etc.), cannot be used alone (Noss, 1990). Indeed, completely different communities can be characterized by the same species-richness and diversity values. Our review analysis also pointed out an absence of consensus on indicators of community structure integrity: various multivariate analyses and various similarity-dissimilarity indices are widely used (52.5% and 20% of the studies respectively) (Appendix B). Nevertheless, all these indicators can have some drawbacks. Multivariate analyses are designed to maximize the variance while reducing the number of dimensions and provide a good overview of plant community composition and help to distinguish different plant communities (Borcard et al., 2011; McGarigal et al., 2000). While some methods allow us to significantly distinguish groups (Borcard et al., 2011; McArdle and Anderson, 2001), it is difficult to assess the magnitude of these differences between groups and impossible to compare, for example, the same restoration technique in two different ecosystems. Moreover, these types of analyses are not commonly used by practitioners because it is difficult to communicate their results to the general public. One-dimension measure, even if it summarizes more (and consequently reduces the amount of) information, is easier to interpret and can solve the problem of assessing magnitude differences. Examples of one-dimension community comparison measure are the widely used similarity-dissimilarity indices (such as Sorensen or Bray–Curtis) but these indices can be difficult to interpret: the dissimilarities can be attributed either to lower abundances of target species (i.e. species present in the reference community), or to higher abundances of target or non-target species compared with the reference community. These two explanations, which can occur concurrently, do not have the same implications in terms of community dynamics and hence of further management (Luken, 1990).

The objective of this work is therefore to develop an assessment method of community structure integrity after restoration (i.e. to measure restoration success) or after disturbance (i.e. to measure resilience) that measures the two types of community dissimilarities: lower and higher abundances in the restored or degraded community compared to reference communities. We have developed two indices giving additional insights on community states: the first index measures the proportion of the species abundance in the reference community represented in the restored or degraded community, and the second index measures the proportion of the species abundance in the restored or degraded community which is higher than in the reference community. We illustrate the use of these indices with fictitious communities, with an application to resilience and with an application to restoration in order to discuss the contribution of the new indices compared with existing ones, their perspective of utilization and limits.

2. Materials and methods

2.1. Indices description

The goal of our indices is to measure resilience or restoration success in a given community (the assessed community, AC), by comparison with a series of communities used as a reference (RC). Using a series of reference communities is crucial, as we expect undisturbed areas to present possible large variations in composition. Each community is characterized by a list of species each associated with a number (n) which reflects their abundance on a given area at a given date: size, biomass, abundance coefficient, percentage of cover, etc. The assessed community may be composed of target species (Clewell and Aronson, 2007), i.e. species present in the reference community, but also of non-target species. The idea behind our indices is to distinguish the species lower in abundance in the assessed community than in the reference communities, from the species higher in abundance in the assessed community than in the reference communities.

For a given species i, we note $\Delta i,j = |ni,\mathrm{AC} - ni,j|$ the absolute difference between the abundance in the assessed community and the abundance in reference community j. We indicate with a subscript whether the abundance in the assessed community is lower ($\Delta^-_{i,j}$) or higher ($\Delta^+_{i,j}$) than in the reference community.

We define 3 indices:

1) The Community Structure Integrity Index (CSII) measures the average proportion of species' abundance in the reference communities represented in the assessed community, and is defined as:

$$\mathrm{CSII} = \overline{\left[\frac{\sum_{i=1\ldots S}(n_i - \Delta^-_{i,j})}{\sum_{i=1\ldots S} n_{i,j}}\right]}^{j=1\ldots K}$$

with S the total number of species over all communities and K the total number of reference communities. The overbar stands for the arithmetic mean over all reference communities. The CSII index thus focuses on the "deficit" of abundance in the assessed community. It takes values between 0 and 1, and equals 1 when all species in the assessed communities are at least as abundant as in the reference communities.

2) The normalized Community Structure Integrity Index ($\mathrm{CSII}_{\mathrm{norm}}$) is a normalized version of CSII. Indicators which represent measurable portions of a reference are the easiest to interpret and therefore the most convincing (Balmford et al., 2005; Duelli and Obrist, 2003). We calculate a normalized value of CSII as: $\mathrm{CSII}_{\mathrm{norm}} = \frac{\mathrm{CSII}}{\mathrm{CSII}_{\mathrm{RC}}}$ with $\mathrm{CSII}_{\mathrm{RC}}$ the arithmetic mean of CSII calculated over all reference communities. Hence, reference communities have an average $\mathrm{CSII}_{\mathrm{norm}}$ value of 1; this allows a meaningful comparison of $\mathrm{CSII}_{\mathrm{norm}}$ values across ecosystems with different heterogeneity of reference communities.

3) The Higher Abundance Index (HAI) measures the average proportion of species' abundance in the assessed community higher than the reference communities, and is defined as:

$$\mathrm{HAI} = \overline{\left[\frac{\sum_{i=1\ldots S} \Delta^+_{i,j}}{\sum_{i=1\ldots S} n_{i,\mathrm{AC}}}\right]}^{j=1\ldots K}$$

where the overbar stands for the arithmetic mean over all reference communities. HAI considers both target species having a

higher abundance in the assessed community than in the reference community and non-target species.

No normalized version of HAI was developed as it is already a relative value to the whole assessed community structure.

We calculated the 3 indices and compared them to standard indicators in three case studies: one with fictitious communities, one in which resilience is assessed after disturbance, and one in which restoration is assessed.

2.2. Fictitious case study

New methods need to be tested rigorously before being applied to real data. We created fictitious communities which allowed us to confirm that the new indices show differences when they occur and do not show differences when they do not occur. We defined 10 types of fictitious communities: one reference, and nine assessed community types where the increase in target species abundances (T0, T0.5 and T1 having respectively 0×, 0.5× and 1× the abundance of target species in the reference) and the increase in non-target abundances (N0, N0.5 and N1 having respectively 0×, 0.5× and 1× the abundance of non-target species) were crossed, resulting in the following community types: T0N0, T0N0.5, T0N1, T0.5N0,T0.5N0.5, T0.5N1, T1N0, T1N0.5 and T1N1 (Fig. 1). As it is important that fictitious communities are the closest to what they are supposed to simulate (Zurell et al., 2010), we simulated 10 samples for each community type (representing the samples which could be surveyed in a community assessment), within which species abundances were characterized by means and variances similar to those found in an example of real plant communities assessed in a restoration context (Jaunatre et al., 2012).

2.3. Application to the resilience of a Mediterranean steppe after ploughing

La Crau area is the last xeric steppe in south-eastern France (ca. 10,000 ha; c. 43°33′ N, 4°52′ E) and has been shaped by (i) a Mediterranean climate: a mean annual temperature of 15 °C, a variable annual sum of precipitation between 400 and 600 mm concentrated in autumn and spring, with four months of summer drought, and more than 110 days with a >50 km h^{-1} wind; (ii) 40 cm deep soil composed with about 50% of silicaceous stones overlying a conglomerate layer, making the alluvial water table unavailable to the roots of plants and (iii) itinerant sheep grazing over a period of several thousand years (Buisson and Dutoit, 2006; Devaux et al., 1983). Although this area is protected by a French National Reserve status, a 5.7 ha area was accidentally ploughed in August 2010. Once the Reserve authorities were aware of the incident, the area was steamrollered in order to reduce the effects of ploughing. Vegetation relevés were carried out in order to assess the impact of such a disturbance: nine 4 m^2 quadrats were surveyed in the ploughed area and the unploughed area (reference community) in May 2011. Standard indicators and the three indicators presented above were calculated for both areas.

2.4. Application to the restoration by hay transfer of a Mediterranean meso-xeric grassland

The Camargue natural areas (Rhône Delta, south of France, 140,000 ha) have drastically declined with the combined effects of industrialization and agricultural development (Lemaire et al., 1987). Currently, opportunities arise to rehabilitate them on abandoned cultivated plots. The 70 ha Cassaïre site (c. 43°31′ N, 4°44′ E), is mostly composed of 70 former rice fields. The upper elevation of the site (3 m above sea level) is currently being restored by transferring hay from reference xero-halophytes communities of the Tour du Valat domain (Mesléard et al., 2011) located 10 km away from the restoration site. The hay was previously gathered by air-vacuuming in summer 2010 and transferred on five mesocosms (15 m × 5 m × 40 cm deep) randomly disposed on the site. Hay material was applied on a 2 m × 10 m plot (hay density = 11.5 g m^{-2}). Five control mesocosms where no hay transfer was applied were also randomly disposed. A vegetation survey was carried out in the hay transfer and the control using 50 cm × 50 cm grids in each mesocosm subdivided into 25 10 cm × 10 cm cells for each species recorded, giving a frequency. Five grids were also randomly surveyed in the reference community.

2.5. Analyses

We calculated standard indicators for the three case studies: species richness, Shannon index, Shannon evenness (Pielou, 1969) which are indicators of diversity, and Sorensen similarity and Bray–Curtis similarity (i.e. 1-Bray–Curtis dissimilarity index) which are both indicators of composition. The Sorensen index does not take abundances into account, while the Bray–Curtis index does (Borcard et al., 2011). In order to have one value of similarity for each assessed community sample, we calculated the mean of

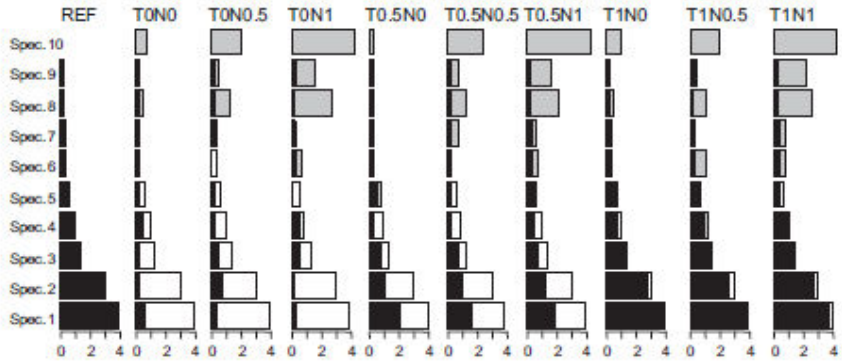

Fig. 1. Structure of the eight fictitious communities. White areas are missing abundances, black areas are abundances up to reference community abundances and grey areas are abundances higher than the reference community abundances. REF is the reference community, and the nine others are assessed community types where the increase in target species abundances (T0, T0.5 and T1 having respectively 0×, 0.5× and 1× the abundance of target species in the reference) and the increase in non-target abundances (N0, N0.5 and N1 having respectively 0×, 0.5× and 1× the abundance of non-target species). Data are mean ± SE, two bars with no letter in common are significantly different according to Tukey Honestly Significant Differences comparisons ($p < 0.05$).

Table 1
Description of standard indicators and of the new indices developed.

Indicators	Description of the indicators
Species-richness	Number of different species recorded in a delimited area.
Shannon index	Shannon index is a diversity index which expresses a ratio of proportion of species abundance relative to the whole community. The more one species dominates the community compared to other species, the higher Shannon index is. It is limited between 0 and a maximum potential which increases with species-richness.
Shannon evenness	Shannon evenness maximum potential value depends on the species-richness of the assessed community. Shannon evenness is relative to this potential maximum and is therefore limited to 1.
Sorensen similarity index	Sorensen similarity index is a similarity index between two samples which take into account only composition, not species abundance. It increases when two communities are close and is limited between 0 and 1.
Bray–Curtis similarity index	Bray–Curtis similarity index is a similarity index between two samples which take into account composition and species abundance. It increases when two communities are close and is limited between 0 and 1. Usually, Bray–Curtis dissimilarity is used but for clarity's sake, we used the similarity (1-Bray–Curtis similarity).
Community Structure Integrity Index (CSII)	CSII is an index calculated between a sample and one or several samples of a reference community. It measures the proportion of the species abundance in the reference community represented in the assessed community. It increases when target species abundance increases until their abundance reach those of reference community. It is limited between 0 and 1.
Normalized Community Structure Integrity Index ($CSII_{norm}$)	$CSII_{norm}$ is similar to the CSII but is normalized in a way that when it is calculated in the reference community it takes a 1 value. It is also limited between 0 and 1.
Higher Abundance Index (HAI)	HAI is an index calculated between a sample and one or several samples of a reference community. It measures the proportion of the species abundance in the assessed community which is higher than in the reference community. It increases when non-target species abundance increases or when target species abundance increases above their abundance in reference community. It is limited between 0 and 1.

similarities between that sample and each reference community sample. Then, in order to have one value of similarity for each reference community sample, we calculated the mean of similarities between that sample and each reference community sample. We also calculated the three new indices (HAI, CSII and $CSII_{norm}$,) for the three case studies.

After checking conformity to parametric conditions we performed *T*-tests for the Mediterranean steppe case study and an ANOVA followed by Tukey HSD post hoc tests for the fictitious and the Mediterranean xero-halophyte grassland case study to compare indicators between communities.

All calculations and analyses were performed with the package "stats" and "vegan" in R 2.13.0 (R Development Core Team, 2011) and we used the R code given in Appendix B for our three new indices (CSII, $CSII_{norm}$ and HAI) calculations and abundances plotting.

3. Results

3.1. Fictitious case study

Species-richness and Shannon index increased or decreased independently of which species occur in the assessed community. Obviously, the smaller species-richness was found in the T0N0 community and the highest species-richness in the T1N1 community (Figs. 1 and 2). The Shannon evenness, which is independent of species-richness, was the highest in the community with low abundances, and was not significantly different between the reference and the other community types. Sorensen similarity and Bray–Curtis similarity increased when target species abundances increased, but only Bray–Curtis similarity decreased when non-target species abundances increased. There was no significant difference in Bray–Curtis similarity indices between the T0.5N0 community, where target species abundances was lower than in the reference and non target species abundances null, and the T1N1 community, where target species abundances were equal to the reference and non target species abundances higher. CSII and $CSII_{norm}$ increased only when target-species abundances increased and were not significantly different from the reference when all the target species had the same abundance as in the reference. CSII and $CSII_{norm}$ were not influenced by the increase in non-target species abundances. On the contrary, HAI was significantly influenced by the increase in non-target species but not by target species abundances. However, when the overall abundance of community decreased, the HAI increased.

3.2. Resilience of a Mediterranean steppe

The reference and ploughed communities shared numerous species (Fig. 3), as expressed by their similar species-richness (Table 1). However many species have different abundances: some have higher abundance in the reference community (e.g. *Brachypodium distachyon*) or are absent in the ploughed community (e.g. *B. retusum*), whereas some have higher abundances in the ploughed community (e.g. *Bromus madritensis*), or were not recorded at all in the reference community (e.g. *Polycarpon tetraphyllum*). These differences in abundance were poorly shown by diversity indices: Shannon index was significantly different (1.68 ± 0.04 in the reference vs. 1.61 ± 0.07 in the ploughed community; $p = 0.04$) but Shannon evenness was not significantly different ($p = 0.38$). As for indices dealing with community composition (Sorensen similarity index, Bray–Curtis similarity index) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance Index) we found significant differences between the reference and ploughed communities (Table 1). Sorensen and Bray–Curtis similarities were higher in the reference community than in the assessed community (ploughed community). The mean $CSII_{norm}$ reached 0.41 in the ploughed community meaning that 59% of the reference community was destroyed by the ploughing event. The reference community had a mean $CSII_{norm}$ of 1, while it had a mean CSII of 0.71. The reference community had a mean HAI of 0.29 significantly different from the ploughed community mean HAI of 0.64 meaning that 64% of the abundance in the ploughed community came from species in higher abundance than in the reference communities.

3.3. Restoration of a Mediterranean meso-xeric grassland

The restored hay transfer community shared more species with the reference community than with the control community (Fig. 4). However, as in the resilience case study, some species showed different abundances: some had higher abundance in the reference community (e.g. *Galium murale*) or were completely absent in the restored community (e.g. *B. phoenicoides*) whereas some had higher abundances in the restored community (e.g. *B. hordeaceus*), or were not recorded in the reference community (e.g. *Polygonum*

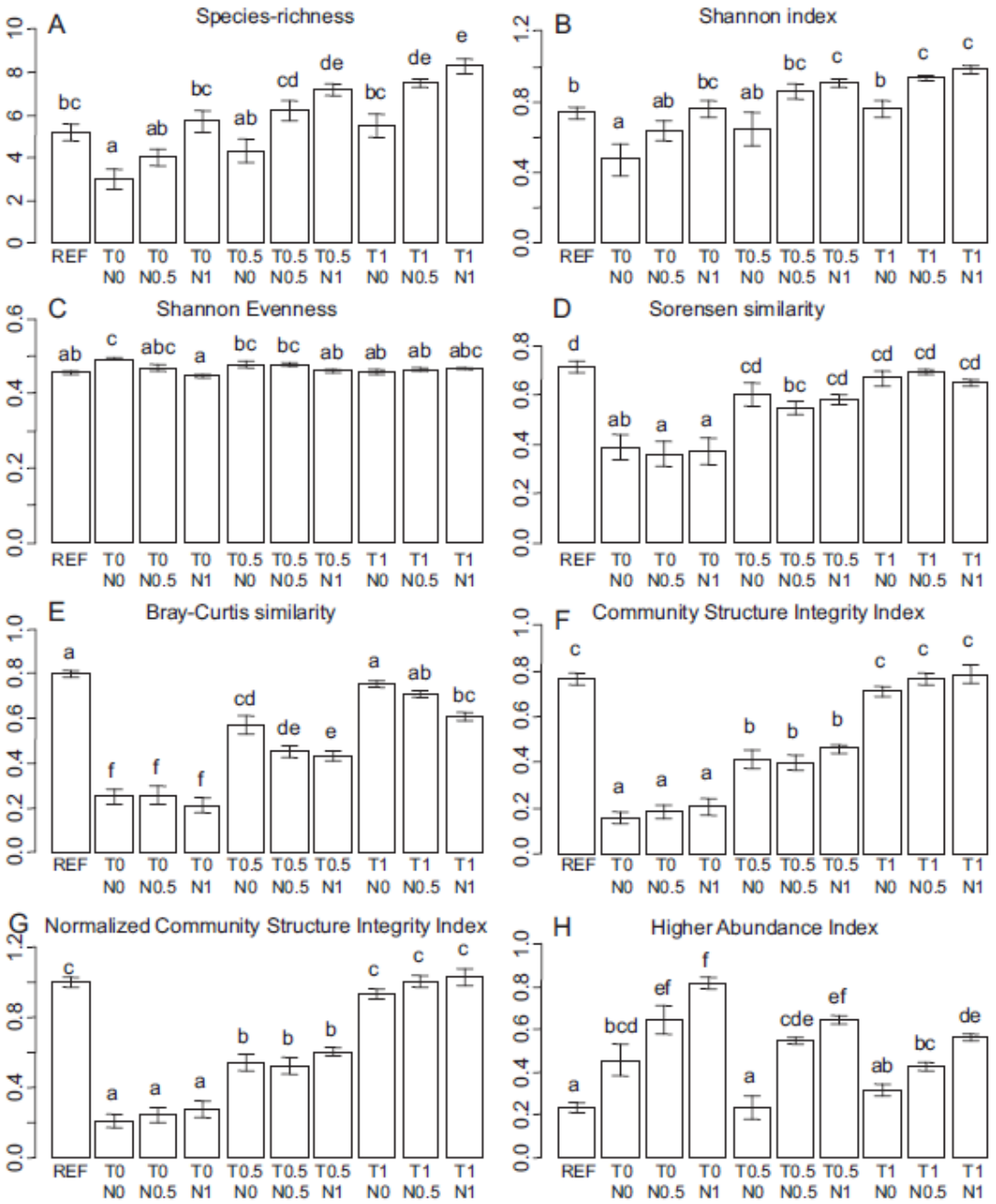

Fig. 2. Comparison of standard indicators (Species-richness, Shannon index, Shannon evenness, Sorensen similarity index, Bray–Curtis similarity index (1-Bray–Curtis dissimilarity index) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance Index) in the ten fictitious communities. REF is the reference community, and the nine others are assessed community types where the increase in target species abundances (T0, T0.5 and T1 having respectively 0×, 0.5× and 1× the abundance of target species in the reference) and the increase in non-target abundances (N0, N0.5 and N1 having respectively 0×, 0.5× and 1× the abundance of non-target species). Data are mean ± SE, two bars with no letter in common are significantly different according to Tukey Honestly Significant Differences comparisons ($p < 0.05$).

aviculare). We did not find any differences in the Shannon index and species richness between reference and hay transfer community (Table 2). Nevertheless, Sorensen similarity index, Bray–Curtis similarity index and the three new indices ($CSII_{norm}$, CSII and HAI) were significantly different between the 3 communities ($p < 0.001$ for the five indices). Sorensen and Bray–Curtis similarities were the highest in the reference community and the lowest in the control. The mean $CSII_{norm}$ of the control was 0.01, meaning that only

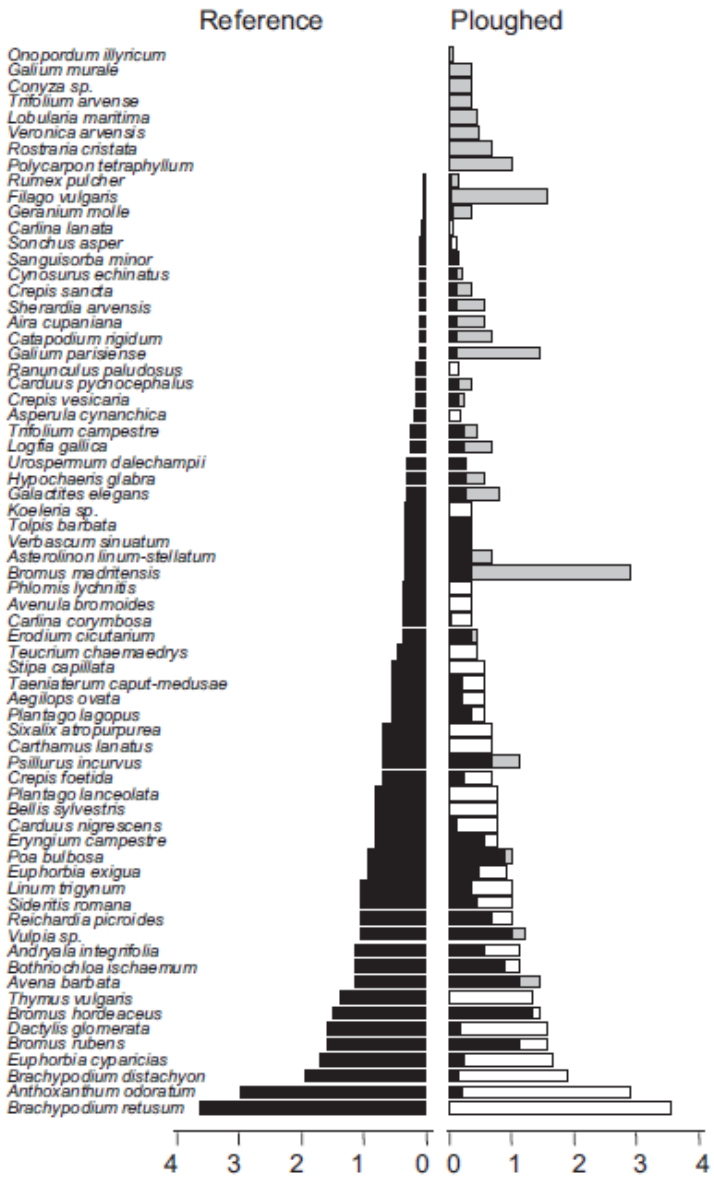

Fig. 3. Mean abundances of reference community and ploughed communities (assessed community) (n= 9). Black areas represent mean abundances in the reference communities. White areas represent mean missing abundances in the ploughed community, grey areas represent mean abundances in the ploughed community up to the mean abundances in the reference community and yellow areas represent abundances which are higher than in the reference community. For clarity purposes, only species which occur in more than 3 samples are shown (67 of the 119 species).

1% of the reference community abundance was expressed in this community. It reached a mean of 0.20 for the restored community, meaning that according to our index, 20% of the reference community has been restored. In the reference community the mean of the $CSII_{norm}$ and the CSII were respectively of 1 and 0.67. In this reference community the value of the mean HAI (0.32) was significantly different from the restored or the control (respectively 0.77 and 0.99) meaning the control community corresponded to 99% of the abundance of target species higher than the reference community or of non-target species. Table 3

4. Discussion

4.1. Comparison of standard indicators with CSII and HAI

Among the numerous indicators used to assess diversity (functional diversity, β diversity, etc.), some standard indicators are widely used in conservation biology (species-richness, Shannon or Shannon evenness) and provide useful information on community states. Nevertheless, when measuring resilience or restoration, they have to be cautiously interpreted. In our case studies we

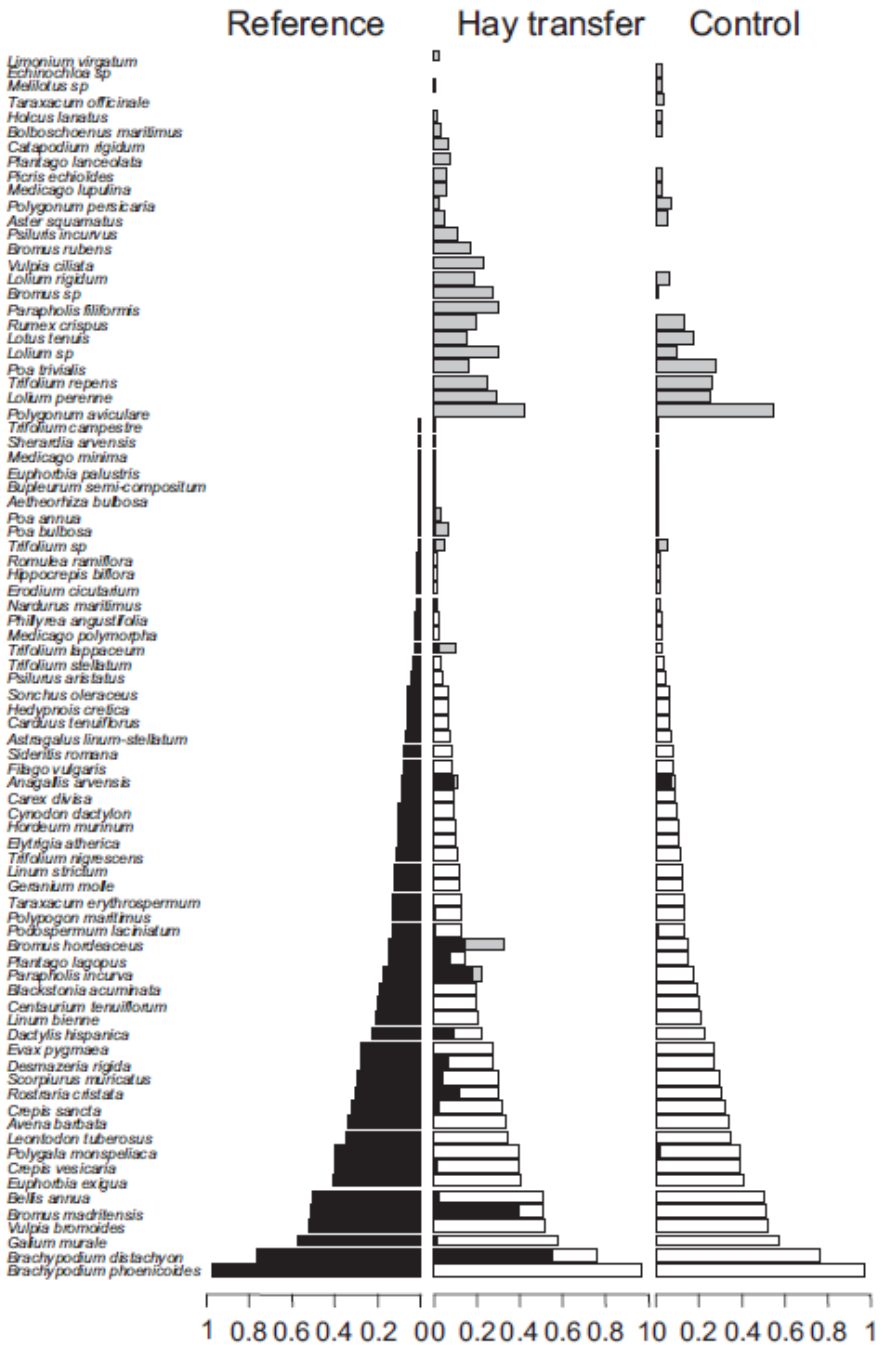

Fig. 4. Mean abundances of reference, hay transfer and control communities ($n = 5$). Black areas represent the mean abundances in the reference communities, white areas represent mean missing abundances in hay transfer and control communities, grey areas represent mean abundances in ploughed community up to the mean abundances in the reference communities and yellow areas represent mean abundances which are higher than in the reference communities. For clarity purposes, only species which occur in more than 2 samples are shown (83 on 97 species).

found no significant differences in the species-richness and evenness between the restored or ploughed community and their respective references, although the communities showed great differences in composition. More seriously, sometimes diversity indicators are higher in the assessed community than in the reference, despite the fact that the community is dominated by non-native or ruderal species (Balcombe et al., 2005). Even if species-richness and evenness were similar in the assessed

Table 2
Comparison of standard indicators (species-richness, Shannon index, Shannon evenness, Sorensen similarity index and Bray–Curtis similarity (i.e. 1-Bray–Curtis dissimilarity)) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance Index) between the reference community and the ploughed area.

	Reference	Ploughed area	*t*	*df*	*p*	
Species-richness	33.78 ± 2.88	29.67 ± 4.43	1.90	14	0.078	
Shannon index	1.68 ± 0.04	1.61 ± 0.07	2.27	13	0.041	*
Shannon evenness	0.48 ± 0	0.48 ± 0	0.92	14	0.375	
Sorensen similarity index	0.71 ± 0.02	0.4 ± 0.08	9.71	9	<0.001	***
Bray–Curtis similarity index	0.71 ± 0.02	0.31 ± 0.06	14.50	10	<0.001	***
Community Structure Integrity Index	0.71 ± 0.03	0.29 ± 0.08	12.00	10	<0.001	***
Normalized Community Structure Integrity Index	1.00 ± 0.04	0.41 ± 0.11	12.00	10	<0.001	***
Higher Abundance Index	0.29 ± 0.03	0.64 ± 0.04	−17.47	14	<0.001	***

Reported values are means ± confidence interval (95%).
t is the statistic of the *t* test, *df* the degree of freedom.
p value (no sign: $p > 0.05$).
* $p < 0.05$.
*** $p < 0.001$.

communities and in their respective reference, we cannot consider that the meso-xeric grassland has been fully restored by hay transfer and that the ploughed steppe has fully recovered after one year. Similarity indices, which permit the comparison of the composition of two communities, are used to assess restoration or resilience (Appendix A). Some similarity indices, however, do not take abundance into account (e.g. Sorenson, Ochiai, etc. (Borcard et al., 2011)). Those indices cannot detect dissimilarities between two communities of identical composition but of different structure, as our fictitious communities example shows. Structure may be a determinant for ecosystem functioning (Chapin et al., 1997). Indices which depend on community structure should thus be preferred when assessing resilience or restoration (e.g. Bray–Curtis, etc. (Borcard et al., 2011)). In our case studies the Bray–Curtis similarity index is the standard indicator which expresses the largest difference between reference and assessed communities. Nonetheless, such indices, when deviating from the maximum similarity (i.e. 1 for similarity indices, 0 for dissimilarity indices), may reflect two different kinds of patterns: the species in the assessed community may have lower abundances than those in the reference community, or they may have higher abundances. Our three new indices permit disentangling these two different patterns, which can occur simultaneously. This is particularly illustrated by the fictitious case study. Indeed, when the abundances were higher in the assessed than in the reference community, Bray–Curtis similarity decreased. On the contrary, the CSSI does not depend on abundances that were higher than in the reference community and thus does not decrease. The similarity decreasing is expressed in the Higher Abundance Index, which then deviates from 0. The ploughed steppe community and the restored xero-halophytic grassland community had $CSII_{norm}$ of 0.41 and 0.20 respectively meaning that according to our indices, assessed communities contain 41% and 20% of abundances of their respective reference communities. Their mean HAI were 0.64 for the ploughed steppe community and 0.77 for the restored meso-xeric grassland community, meaning that, according to our indices, the assessed communities contained 64% and 77% of their respective total abundance which are higher abundances (i.e. non-target species or abundances of target species are higher than mean reference abundances).

4.2. Contribution of CSII and HAI to community assessment interpretation

The choice of an indicator depends on what one wants to measure, and on the objectives with which the measures are taken (Duelli and Obrist, 2003). Moreover, (Balmford et al., 2005) advocates using indicators that are rigorous, repeatable, and widely and easily understandable. $CSII_{norm}$ and HAI indices both represent

Table 3
Comparison of standard indicators (species-richness, Shannon index, Shannon evenness, Sorensen similarity index and Bray–Curtis similarity (i.e. 1-Bray–Curtis dissimilarity)) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance index) between the reference community, the hay transfer community and the control community.

	Reference	Hay transfer	Control	*F*	*df*	*p*	
Species-richness	34.80 ± 4.95 a	25.00 ± 12.49 a	9.60 ± 8.31 b	18.69	2	<0.001	***
Shannon index	1.60 ± 0.09 a	1.41 ± 0.22 a	0.85 ± 0.68 b	8.71	2	0.005	**
Shannon evenness	0.45 ± 0.02	0.45 ± 0.03	0.44 ± 0.05	0.26	2	0.77	NS
Sorensen similarity index	0.71 ± 0.05 a	0.25 ± 0.16 b	0.03 ± 0.07 c	102.90	2	<0.001	***
Bray–Curtis similarity index	0.59 ± 0.06 a	0.16 ± 0.13 b	0.01 ± 0.01 c	128.86	2	<0.001	***
Community Structure Integrity Index	0.67 ± 0.07 a	0.13 ± 0.13 b	0.00 ± 0.01 c	170.56	2	<0.001	***
Normalized Community Structure Integrity Index	1 ± 0.11 a	0.20 ± 0.19 b	0.01 ± 0.02 c	176.56	2	<0.001	***
Higher Abundance index	0.32 ± 0.04 a	0.77 ± 0.18 b	0.99 ± 0.02 c	94.10	2	<0.001	***

Reported values are means ± confidence interval (95%).
Values on a line with a common letter are not significantly different (Tukey HSD test with a *p*-value adjustment according to Bonferroni's method).
F is the statistic of the ANOVA test, *df* the degree of freedom.
p the *p* value (NS: $p > 0.05$).
** $p < 0.01$.
*** $p < 0.001$.

easily understandable measurements for conservation biologists of a community state: $CSII_{norm}$ is the proportion of the reference community structure which can be found in the assessed community whereas HAI is the proportion of the assessed community structure that is represented by higher abundances than in the reference community. Knowing whether a community has a "deficit" of target species abundance or is characterized by higher abundances is of primary interest for practitioners who want to manage ecological succession (Kiehl and Pfadenhauer, 2007; Luken, 1990).

4.3. Applications of indices to restoration ecology and biological conservation

Low values of CSII express a lack of target species in the assessed community. Therefore identifying the reasons why these species do not reach the reference community abundances is of primary interest. If target species do not disperse, the propagule source may be too far away or the target species do not produce sufficiently dispersible propagules: management can be focused on strengthening dispersion processes (see Kiehl et al. (2010) for review). For example, the restored meso-xeric grassland case study shows that dispersion strengthening by hay transfer increases CSII value. Environmental conditions may be too far from the growth optimum of target species, in which case management should involve trying to restore suitable conditions (Bakker and Berendse, 1999; Dorland et al., 2005). Target species may also be in competition with non-target species (D'Antonio et al., 2003), which will be expressed with high values of HAI. Management should then involve trying to decrease abundances of these species with higher abundances, whether it concerns target species or not (Donath et al., 2003; Murray and Marmorek, 2003). More than a static measurement, these indices may be used to monitor the succession of assessed communities. Increasing CSII values could show that dispersion strengthening is not necessary. On the contrary, an increase of HAI, even if the values are low, can indicate the need for managing higher abundance (Donath et al., 2003; Haywood, 2009). In both real case studies, HAI are significantly higher than in the reference community. If HAI increases during forthcoming years, the actual site management, extensive sheep grazing, will have to be adapted to reduce higher abundance. Otherwise these species with higher abundance may have a negative feedback on the CSII values and thus threaten the maintenance of community integrity success.

4.4. Limits and constraints of CSII and HAI use

Particular attention should be paid to data gathering before performing indices calculations. Whether it is for assessing resilience or restoration efficiency, the definition and characterization of reference ecosystems are crucial (White and Walker, 2008). A broad part of ecological restoration literature deals with this issue (Egan, 2001; Ehrenfeld and Toth, 1997). In order to avoid bias in HAI or CSII calculations, similar community characterization protocol should be used in reference and assessed ecosystems (same sample size, working effort, plant identification skills and date of sampling). Communities are not static entities and, at least in the framework of restoration, the reference should be all the manifested or potential states that occur within a given historical and spatial variation (Landres et al., 1999; Society for Ecological Restoration International Science and Working Policy Group, 2004). Therefore, reference community characterization should take into account the natural variability of the reference, both spatially and temporally (White and Walker, 2008). Calculation of CSII and HAI should be performed in both the reference and assessed communities. Indeed the indices give information on the reference community variability and heterogeneity and allow statistical analyses comparing the reference and assessed communities. These comparisons provide an overview of the assessed community but do not account for the whole complexity of an ecosystem: functional, spatial or dynamic attributes are eluded. Therefore these indices should be used in addition to standard indicators or more specific ones adapted to each case study (see for example Raab and Bayley (2012)). Moreover, in a context of the evaluation of a restoration project, assessment of one community of the whole ecosystem is not sufficient to draw conclusions on the project. Several communities should be assessed (i.e. plants, insects, birds, mammals, microbes, etc.), as well as environmental characteristics (i.e. soil chemistry, disturbance regime, etc.) or landscape-scale indicators (i.e. fragmentation, etc.) (Palmer et al., 2005; Tasser et al., 2008).

4.5. Perspective of use and development of CSII and HAI

All species do not necessarily have the same status in a community, whether they could exert a more significant role in ecosystem functioning or services (Bullock et al., 2011; Funk et al., 2008) or they could be of high conservation value. It could have been relevant to give more weight to high conservation value species in the calculation of CSII indices or to give more weight to species with a high invasion potential for the HAI. However, these resulting indices would deviate from the original goal of these indices: measuring in an easily interpretable way the difference from a reference community.

To our knowledge, no meta-analyses have tried to measure the abilities of ecological restoration projects to restore reference community integrity. It has been proved that restoration exerts a significant positive effect on diversity or ecosystem services (Benayas et al., 2009). Regarding the high differences sometimes existing between standard indicators and CSII in our case studies, it would be interesting to perform these indices calculations in such meta-analyses.

Metaphorically speaking, if we compare restoration with assembling a jigsaw puzzle, species-richness would be equivalent to the colour palette of the puzzle and Shannon index, or evenness, would be the correct equilibrium of colours, whereas CSII could be compared to the number of correct pieces of the puzzle. This metaphor leads to two comments: (1) It seems obvious that even the correctly balanced colour palette is not enough to complete the puzzle if 50% of the pieces are missing and (2) Even with all the pieces, they have to be assembled adequately to obtain the desired picture. To our knowledge, there is no indicator which measures this community configuration (apart from random/aggregated distribution) although it has been proved to exert a significant effect on ecosystem functioning (Maestre et al., 2012). Consideration of how to measure the state of a community in a framework of restoration or resilience assessment should be continued to set realistic and measurable goals for ecosystem management as noticed by Ehrenfeld and Toth (1997).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2013.01.023.

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Annexe 2: Espèces présentes dans la banque de grains du Cassaïre, les pelouses meso-xériques de reference, le materiel vegetal transféré, les mésocosmes transférés et les mésocosmes témoins. Les espèces cibles sont indiquées en gras.

Species recorded	In soil seed bank of the Cassaïre site	In reference grassland	In Hay material	In hay transfer slopes	In control slopes
Aegilops ovata			×	×	
Aetheorhiza bulbosa			×	×	
Ammania coccinea	×				
Anagalis arvensis	×	×	×	×	×
Aster squamatus	×			×	×
Asterolinon linum-stellatum		×			
Atriplex prostata				×	
Avena barbata		×			
Bellis annua		×	×	×	
Blackstonia acuminata		×	×		
Bolboschoenus maritimus				×	×
Brachypodium distachyon		×	×	×	
Brachypodium phoenicoides		×	×	×	
Bromus diandrus				×	×
Bromus hordeaceus		×	×	×	
Bromus madritensis		×		×	×
Bromus rubens				×	
Bromus sp				×	×
Bromus sterilis				×	×
Bupleurum semicompositum		×	×	×	
Carduus tenuiflorus		×			
Carex divisa	×	×	×		
Carex otrubae				×	
Catapodium rigidum		×	×	×	
Centaurium spicatum	×		×		
Centaurium tenuifolium		×			
Chenopodium album				×	×
Cirsium arvense				×	×
Conyza sumatrensis	×				
Coronopus squamatus					×
Crepis sancta		×	×	×	
Crepis vesicaria		×	×	×	
Cynodon dactylon		×			
Cyperus difformis	×				
Cyperus eragrostis	×				
Cyperus fuscus	×		×		
Cyperus sp					×
Dactylis hispanica		×	×	×	
Dactylis sp				×	
Daucus carota	×				
Dittrichia viscosa				×	
Echinochloa sp	×			×	×
Elytrigia atherica		×	×	×	
Epilobium tetragonum	×				

Species recorded	In soil seed bank of the Cassaïre site	In reference grassland	In Hay material	In hay transfer slopes	In control slopes
Erigeron canadense	×				
Erodium cicutarium		×			
Euphorbia exigua		×	×	×	
Euphorbia peploides		×			
Evax pygmaea		×		×	
Festuca arundinacea				×	
Filago vulgaris		×	×	×	
Galium murale		×	×	×	
Gastridium ventricosum			×	×	
Geranium molle		×	×	×	
Hainardia cylindrica					
Halimione portulacoides		×			
Hedypnois cretica		×		×	
Hippocrepis biflora		×			
Holcus lanatus	×			×	×
Hordeum marinum		×		×	
Hordeum murinum				×	×
Juncus bufonius	×		×	×	
Juncus lamprocarpus	×		×		
Lactuca saligna				×	×
Lactuca serriola				×	×
Leontodon tuberosus		×	×		
Limonium narbonense			×	×	
Limonium virgatum			×	×	
Lindernia dubia	×				
Linum bienne		×			
Linum strictum		×			
Lolium perenne				×	×
Lolium rigidum				×	×
Lolium sp				×	×
Lotus tenuis	×			×	×
Lythrum hyssopifolia	×				
Medicago lupulina	×			×	×
Medicago minima				×	
Medicago polymorpha	×	×	×	×	
Medicago rigidula			×		
Medicago truncatula		×			
Melilotus inducus	×				
Melilotus sp				×	×
Nardurus maritimus		×		×	
Parapholis filiformis			×	×	
Parapholis incurva		×	×	×	
Parietaria judaica				×	
Paspalum distichum	×				×
Phillyrea angustifolia		×			

Species recorded	In soil seed bank of the Cassaïre site	In reference grassland	In Hay material	In hay transfer slopes	In control slopes
Erigeron canadense	×				
Erodium cicutarium		×			
Euphorbia exigua		×	×	×	
Euphorbia peploides		×			
Evax pygmaea		×		×	
Festuca arundinacea				×	
Filago vulgaris		×	×	×	
Galium murale		×	×	×	
Gastridium ventricosum			×	×	
Geranium molle		×	×	×	
Hainardia cylindrica					
Halimione portulacoides		×			
Hedypnois cretica		×		×	
Hippocrepis biflora		×			
Holcus lanatus	×			×	×
Hordeum marinum		×		×	
Hordeum murinum				×	×
Juncus bufonius	×		×	×	
Juncus lamprocarpus	×		×		
Lactuca saligna				×	×
Lactuca serriola				×	×
Leontodon tuberosus		×	×		
Limonium narbonense			×	×	
Limonium virgatum			×	×	
Lindernia dubia	×				
Linum bienne		×			
Linum strictum		×			
Lolium perenne				×	×
Lolium rigidum				×	×
Lolium sp				×	×
Lotus tenuis	×			×	×
Lythrum hyssopifolia	×				
Medicago lupulina	×			×	×
Medicago minima				×	
Medicago polymorpha	×	×	×	×	
Medicago rigidula			×		
Medicago truncatula		×			
Melilotus inducus	×				
Melilotus sp				×	×
Nardurus maritimus		×		×	
Parapholis filiformis			×	×	
Parapholis incurva		×	×	×	
Parietaria judaica				×	
Paspalum distichum	×				×
Phillyrea angustifolia		×			

Annexe 3: Article sur le Cassaïre. Journal du CNRS, Ingénieuse écologie.

Bilan, trois ans plus tard : « *Nous sommes très satisfaits, car les espèces s'épanouissent, et cela est encore plus impressionnant sur la parcelle greffée. En un an, on ne voyait presque plus la différence entre la steppe d'origine et le site réhabilité.* » Des moutons, ingénieurs eux aussi, se sont chargés des finitions en régulant la pousse des végétaux. Depuis 2010, deux bergers font ainsi régulièrement paître leurs troupeaux sur le site de l'ancien verger.

UN ÉQUILIBRE TRÈS SUBTIL

Happy end en plaine de Crau ? À court terme, sans conteste. Il faut néanmoins noter que l'empreinte écologique de ces deux opérations est loin d'être négligeable : des jours entiers à faire marcher des pelleteuses, et des rotations de camions par centaines. « *Nous veillons toujours scrupuleusement à réduire cette empreinte au minimum,* assure Thierry Dutoit. *Et sommes constamment en recherche du meilleur rapport entre la qualité de la régénération et le coût écologique pour une restauration durable des écosystèmes.* »

Dans ce cas, pourquoi ne pas laisser la nature reprendre ses droits ? Pour réinvestir des territoires gâtés par l'homme, elle est d'une efficacité redoutable. Le site de la centrale de Tchernobyl en est la preuve. Il s'est changé en une jungle luxuriante en

14

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Les chercheurs ont entrepris de recréer un marais à la place d'une ancienne exploitation agricole (14) et testent, pour ce faire, des semences dans une mare expérimentale (15).

Avoir sur le journal en ligne : un reportage **photo** sur les chantiers de la plaine de Crau.

à peine vingt ans. « *Si l'on voulait être naturaliste jusqu'au bout, il serait sans doute plus éthique de s'en remettre à la spontanéité des écosystèmes,* répond le chercheur. *Mais si on laissait faire, voilà ce qu'il pourrait se produire : avant que les sites ne retrouvent leur composition d'origine au bout de plusieurs siècles, ce sont les espèces invasives, ne rendant aucun service particulier à l'homme, qui pourraient s'imposer. Autre problème : des maladies sur les repousses de pêchers pourraient s'y développer, contaminant les cultures avoisinantes. Certes, ce sont des considérations anthropiques mais, aujourd'hui, l'homme fait partie intégrante des agro-écosystèmes. Il faut donc prendre en compte les divers intérêts lorsque l'on entreprend un chantier d'ingénierie écologique.* »

C'est précisément ce qu'ont fait les scientifiques de la Tour du Valat[1], en réhabilitant une ancienne exploitation de riz et de vigne, à 5 kilomètres au sud de la plaine de Crau, en Camargue[2]. Avec pour objectif de retrouver, sur cette parcelle de 70 hectares, un marais similaire à ceux que compte la Réserve naturelle du Vigueirat, toute proche. Et ce, en concertation avec les

15

PROTÉGER LES RIVIÈRES

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→ Dans ces bassins, les chercheurs identifient les couples bactéries-plantes les plus efficaces pour dégrader le glyphosate.

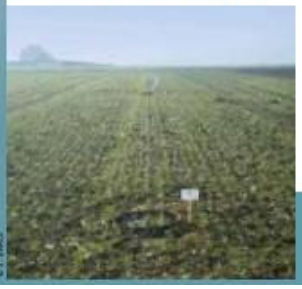
Plusieurs unités, dont le Laboratoire de planétologie et géodynamique de Nantes[1] et le Laboratoire vigne, biotechnologie et environnement[2], se sont penchées sur les bassins d'orage en Alsace. Problème : avant de rejoindre ces réservoirs, l'eau de pluie a pu ruisseler sur des vignobles pentus, se charger en glyphosate, un herbicide courant, et en sédiments pollués du sol. Alors, si le bassin déborde, il déverse de l'eau polluée au glyphosate, et ce parfois directement dans la rivière. Ces réservoirs peuvent pourtant jouer le rôle d'épurateur naturel, car ils contiennent des bactéries et des plantes dont l'association permet de dégrader l'herbicide incriminé. Les chercheurs ont donc sélectionné les couples bactéries-plantes les plus performants dans cette tâche en vue d'en ajouter dans les bassins. Résultat : dans un modèle réduit de laboratoire et dans un petit bassin réel, à Colmar, le système a permis d'éliminer une grande partie du glyphosate. Prochaine étape, valider ce système à l'échelle du bassin d'orage.

1. Unité CNRS/Université de Nantes.
2. Université de Haute-Alsace.

CONTACT :
Thierry Lebeau
› thierry.lebeau@univ-nantes.fr

PRENDRE SOIN DES CULTURES

Le laboratoire Bioemco et l'unité Agronomie[2] évaluent la capacité des vers de terre à servir d'agents de lutte contre certains pathogènes des cultures. Depuis décembre, ils étudient le cas d'un champignon du blé, le piétin échaudage, en pot dans une serre et dans de petits



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chasseurs de la région : pour attirer les canards, ceux-ci ont pour habitude de creuser des marais artificiels et de les remplir d'eau au début de l'été, bien avant le début de la saison de la chasse. Or cette pratique bouleverse les écosystèmes.

CRÉER UN MARAIS DE TOUTES PIÈCES

« Avec ce projet, nous souhaitons réhabiliter un écosystème typique des marais, mais aussi montrer aux chasseurs que l'on peut attirer les canards en remplissant les mares seulement à l'automne, ce qui est beaucoup plus respectueux de la nature », explique François Mesleard, de l'IMBE, scientifique de la Tour du Valat et responsable du projet. Au 20 mars, la première étape, le creusement du marais, était quasiment terminée. Au programme de la seconde : greffer, dans le fond des cuvettes, un sol typique des marais prélevé sur le domaine de la Tour du Valat et, sur les pentes, une pelouse provenant de la réserve du Vigueirat, typique elle aussi. Viendra ensuite le temps de semer des espèces adaptées aux milieux marécageux de la région. *« Avant de démarrer le gros œuvre, nous avons réalisé toute une série de tests »*, précise François Mesleard.

À quelques centaines de mètres du chantier, plusieurs mares expérimentales ont été créées dans le but de tester les greffes des deux sortes de terre ainsi que les semences. *« Nous sommes très satisfaits du résultat,* se félicite Isabelle Muller, doctorante en écologie à l'IMBE : *39 % des espèces cibles se sont bien implantées. »* Pour qu'elles s'installent durablement sans pour autant envahir le paysage et gêner les chasseurs, l'équipe prévoit de réguler leur pousse en introduisant des troupeaux de chevaux. Des ingénieurs probablement aussi brillants que leurs collègues de la Crau : les moutons et les fourmis. **E. B.**

1. La Tour du Valat est le Centre de recherche pour la conservation des zones humides méditerranéennes.
2. De concert avec le Conservatoire du littoral et la Réserve naturelle des marais du Vigueirat.

CONTACTS :
François Mesleard
› francois.mesleard@imbe.fr
Isabelle Muller
› isabelle.muller@imbe.fr

Pour en savoir +

À VOIR :

Du soleil aux molécules, la raffinerie du futur (2011, 20 min), réalisé par Marcel Dalaise, produit par CNRS Images

La Boue et le Roseau (2011, 18 min), réalisé par Claude Delhaye, produit par CNRS Images

› **videotheque.vente@cnrs-bellevue.fr**
› **http://videotheque.cnrs.fr**

JOURNÉES PORTES OUVERTES

Le samedi 2 et le dimanche 3 juin, le CNRS vous invite à découvrir l'ingénierie écologique et ses premiers résultats spectaculaires, partout en France, dans des chantiers, des laboratoires ou au sein d'exploitations agricoles et industrielles.

EN LIGNE
› www.cnrs.fr/inee/communication/journees_ingenierie_ecologique.htm

cylindres implantés dans un champ, à Grignon. Des vers en quantité variable sont ajoutés dans les pots et dans les cylindres pour tester leur interaction avec le champignon. Bilan : ils favorisent la croissance du blé et semblent réduire les attaques du champignon sur la plante. Selon les chercheurs, les vers limiteraient le contact entre le piétin et le blé, notamment en enfouissant des débris végétaux sur lesquels se trouvent les spores du champignon.

1. Unité Inra/AgroParisTech.

CONTACT :
Sébastien Barot
› sebastien.barot@ird.fr

→ Des vers de terre ont été ajoutés dans des cylindres implantés dans ce champ afin d'évaluer leur capacité à lutter contre un champignon pathogène.

VERDIR LES TOITS

Les toits végétalisés, qui recréent de petits espaces verts au cœur des villes, sont à la mode. Mais connaissez-vous les toits écosystémisés ? Luc Abbadie et son équipe planchent actuellement sur ces couverts végétaux qui non seulement rendraient des services à l'homme (en isolant thermiquement les immeubles, en améliorant la qualité de l'eau de ville, en séquestrant du CO_2), mais aussi participeraient à la dynamique de la biodiversité locale et régionale. Les chercheurs sont actuellement en discussion avec plusieurs partenaires, dont la mairie de Paris, pour tester les meilleurs substrats et combinaisons de végétaux sur les toits de quatre

sites où la densité de constructions est forte. Des biosphères entières pourraient donc bientôt coiffer quelques toits franciliens.

CONTACT :
Luc Abbadie
› abbadie@biologie.ens.fr

→ Ce couvert végétal réduit les coûts énergétiques du Chicago City Hall sur lequel il est installé.

C. Z.

Annexe 4: Article sur le Cassaïre. Le Figaro. Juin 2012

LE FIGARO
14 BOULEVARD HAUSSMANN
75438 PARIS CEDEX 09 - 01 57 08 50 00

02/03 JUIN 12
Quotidien Paris
OJD : 316852

Surface approx. (cm²) : 268
N° de page : 11

Camargue : le défi de la réhabilitation des vieilles rizières

Les chasseurs participent, aux côtés des chercheurs, à cette opération d'ingénierie écologique sans précédent.

GUILLAUME MOLLARET
ENVOYÉ SPÉCIAL AU MAS-THIBERT (BOUCHES-DU-RHÔNE)

ÉCOLOGIE Contrairement à une idée reçue, la Camargue n'est pas qu'une vaste zone humide peuplée d'aigrettes et de flamands roses. Ce légendaire triangle de terre formé par les alluvions déposées par le Rhône au fil des millénaires, avant qu'il ne se jette dans la Méditerranée, est aussi en bonne partie dédié à la culture intensive du riz. Mais la médaille a son revers : de nombreuses espèces végétales endogènes se sont raréfiées au fur et à mesure que les marais cédaient la place aux rizières, à partir des années 1960.

Aujourd'hui, bon nombre de ces parcelles agricoles ayant été abandonnées ou vendues, leur réhabilitation représente un enjeu écologique majeur. *« Ces terres contiennent encore trop de résidus d'engrais et de pesticides. En outre, trop d'espèces végétales banales sans intérêt patrimonial se sont développées au détriment de plantes nobles »*, explique François Mesléard, directeur de recherches à la Fondation de la Tour du Valat - un centre de recherche dédié à la conservation des zones humides - et professeur associé au sein d'une équipe du CNRS.

La difficulté pour les scientifiques est qu'il n'existe plus aucune zone abritant l'ensemble des espèces végétales typiques de la Camargue. C'est pour y remédier que l'association des Amis des marais du Vigueirat, chargée de gérer 1 200 hectares de zones humides appartenant au Conservatoire du littoral, a mis en place une expérience pilote d'« ingénierie écologique », au Mas-Thibert (Bouches-du-Rhône), en collaboration avec des chercheurs du CNRS et de la Fondation de la Tour du Valat.

La réhabilitation des marais vise à concilier la chasse et la flore.
D. SHANNON. ONLY FRANCE

240000 euros
C'est le montant de l'opération de mise en eau

À la sortie de ce hameau rattaché à la ville d'Arles, dans le parc naturel régional de Camargue, une trentaine de petits marais d'une dizaine de mètres carrés ont été aménagés sur une ancienne rizière désaffectée. *« Nous y testons diverses règles d'assemblage des communautés végétales pour suivre leur progression et leur résistance face à l'arrivée d'espèces non souhaitées »*, poursuit François Mesléard.

L'objectif est de créer, sur une surface de près de 70 hectares, un marais de référence en matière de biodiversité, qui doit être mis en eau dans quelques mois. L'idéal pour les scientifiques serait que cette zone humide reconstituée, baptisée marais de Cassaïre, serve dans un second de temps de modèle pour la gestion des nombreux marais privés dédiés à la chasse au gibier d'eau, très prisée en Camargue.

Promotion de la flore

« La Camargue est une zone hydrologique artificielle. Aujourd'hui, les chasseurs mettent en eau leur marais juste avant la saison de chasse : une pratique efficace pour attirer le gibier mais qui, malheureusement, ne favorise pas la biodiversité. Seules des espèces banales ou envahissantes arrivent à se faire une place. Il s'agit pour nous de démontrer qu'en opérant à différents moments de l'année et de manière moins coûteuse on peut concilier la chasse avec la promotion de la flore », argumente Jean-Laurent Lucchesi, directeur des Amis des marais du Vigueirat. C'est la raison pour laquelle l'amicale des chasseurs du Mas-Thibert est également associée à la réhabilitation du marais de Cassaïre.

Il faudra attendre environ trois à cinq ans pour savoir si cette opération de mise en eau, d'un montant total de 240 000 euros, est conforme aux hypothèses de départ des scientifiques en matière de retour de la biodiversité. De la qualité des tableaux de chasse dépendra le succès futur de l'initiative. ■

Le CNRS organise ces samedi et dimanche 2 et 3 juin des journées portes ouvertes sur onze sites de recherche en ingenierie écologiques dont celui du Mas-Thibert, a Arles. (www.cnrs.fr)

« Le vent l'emportera »
Noir désir

Résumé

La restauration écologique est considérée comme un des moyens susceptibles d'enrayer la perte de la biodiversité. Les changements d'occupation du sol peuvent être des opportunités pour restaurer des écosystèmes dégradés par les activités agricoles. C'est notamment le cas du projet participatif du domaine du Cassaïre, situé dans le delta du Rhône, qui vise à recréer sur d'anciennes rizières des écosystèmes méditerranéens favorables à l'activité cynégétique. Deux écosystèmes sont plus particulièrement visés, les marais temporaires et les pelouses méso-xériques. Les objectifs de la thèse sont de mettre en évidence les principaux mécanismes concourant à l'installation d'une communauté végétale, de tester des techniques de restauration et d'en évaluer les conséquences pour les communautés végétales mais aussi pour d'autres compartiments de l'écosystème. En l'absence d'espèces cibles dans le pool régional d'espèces, l'introduction de ces espèces est nécessaire en addition de la restauration des conditions abiotiques. L'étrépage et le transfert de sol pour la communauté des marais permettent une augmentation des espèces cibles et de la similarité avec la communauté de référence. Cette technique apparaît moins pertinente pour la communauté d'invertébrés aquatiques. Le succès contrasté du transfert de sol souligne les risques à ne pas privilégier qu'un nombre restreint d'indicateurs de restauration, ne reflétant pas l'ensemble de l'écosystème. L'étrépage de sol suivi d'un transfert de foin semble être une combinaison pertinente pour recréer la communauté végétale de pelouses, même si les résultats obtenus, probablement en raison d'une compétition élevée, sont moins convaincants que pour les marais temporaires. Nos résultats obtenus pour la grande majorité en mésocosmes, s'ils ne concernent que les premières étapes de la restauration, mettent cependant en évidence des techniques de restauration qui paraissent pertinentes pour installer certaines composantes des deux écosystèmes de référence. Ces résultats, par leurs limites, suggèrent néanmoins de privilégier la conservation *in situ* des habitats naturels plutôt que de chercher à les restaurer après qu'ils aient été détruits.

Mots clés : Biodiversité, Ecologie de la communauté, Ecologie de la restauration, Ecosystème aquatique, Ecosystème terrestre, Ecosystèmes méditerranéens, Etrépage de sol, Friches rizicoles, Perturbation, Transfert de foin, Transfert de sol

Abstract

Ecological restoration is considered as one approach to slow down the loss of biodiversity. Changes in land-uses may be an opportunity to restore ecosystems degraded by agricultural activities. This is the case of the participatory project of the Cassaïre site, located in the Rhône delta, which aims at recreating Mediterranean ecosystems favorable to hunting on former ricefields. Two ecosystems are targeted, temporary wetlands and meso-xeric grasslands. The aims of the thesis are to highlight the main drivers of plant community establishment, to test restoration techniques and to evaluate their effects on plant communities but also on other compartments of the ecosystem. In the absence of target species in the regional species pool, the introduction of these species is necessary in addition to the restoration of abiotic conditions. Topsoil removal and soil transfer for wetland communities allow an increase of target species and of similarity with the reference community. This technique appears to be less relevant for aquatic invertebrate community. The contrasted successful of soil transfer highlights the risks of favoring some indicators of restoration success, as they may not reflect the entire ecosystem. Topsoil removal and hay transfer seem to be a relevant combination to recreate grassland plant community, although the results obtained are less convincing than for temporary wetland, probably due to high competition. Our results, obtained in mesocosms, even if they relate only to the early stages of recovery, provide restoration techniques that seem relevant to establish some components of the two reference ecosystems. These results, by their limitations, however, suggest focusing on *in situ* conservation of natural habitats rather than trying to restore them after they were destroyed.

Keywords: Biodiversity, Community ecology, Restoration ecology, Aquatic ecosystem, Terrestrial ecosystem, Mediterranean Ecosystems, Topsoil removal, Former ricefield, Disturbance, Hay transfer, Soil transfer